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Breakdown of Food by Early Fossil Primates, Assessed with the Aid of a
Machine that Simulates Mastication

by

Jonathan Marcus Glen Perry



A thesis submitted to the Faculty of Graduate Studies and Research in partial
fulfillment of the requirements for the degree of Master of Science

in

Systematics and Evolution

Department of Biological Sciences

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University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Breakdown of Food by Early Fossil Primates, Assessed with the Aid of a Machine that Simulates Mastication submitted by Jonathan Marcus Glen Perry in partial fulfillment of the requirements for the degree of Master of Science in Systematics and Evolution.

Abstract

To infer diet in early primates, I built a machine that simulates mastication. This machine models the actions of masticatory muscles on the thick-tailed bushbaby, *Otolemur crassicaudatus*. The masticatory forces in this species are well known and mastication is primitive for Primates. Nineteen post-canine dentitions – each representing a separate species - were used separately in this machine to test fourteen kinds of food. Masticatory performance was assessed by determining the size distributions of chewed fragments.

Three commonly used methods for inferring diet (referred to as Seligsohn's method, Kay's method and Evans and Sanson's method) from molar morphology were applied to the test dentitions. To assess their predictive power, results obtained using these methods were compared to masticatory performances.

Methods that measure the sharpness of cusps and cusp tips are accurate, but apply to few foods and dental features. Methods that integrate several molar dimensions apply to several foods and dental features but are somewhat inaccurate.

Several hypotheses about the diets of early primates are questioned. Late Paleocene Plesiadapiformes (?Primates) were probably not primarily insectivorous; they probably concentrated on plant parts, especially nuts, seeds and leaves. Some adapids (Adapidae, Primates), some omomyids (Omomyidae, Primates) and the late-occurring plesiadapiform *Phenacolemur praecox* probably concentrated on fleshy fruit. Other adapids and omomyids probably were insectivore-graminivores. Relative to plesiadapiforms, Eocene true primates are marked by greater dietary specialization. Performances of extant test species reflected their known diets. Flat dentitions are not specialized for fruit: pointy dentitions are not specialized for insects.

This experiment provides an independent means to infer diet and it tests established methods that rely on dental morphology alone.

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List of abbreviations

Institutional abbreviations

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
DMNH	Denver Museum of Natural History
MNHN	Muséum National d'Histoire Naturelle
UAAC	University of Alberta Anthropological Collection
UALVP	University of Alberta Laboratory for Vertebrate Paleontology
UAMZ	University of Alberta Museum of Zoology
UCM	University of Colorado Museum
UCMP	University of California Museum of Paleontology
UCMZ	University of Calgary Museum of Zoology
UKMNH	University of Kansas Museum of Natural History
UMMP	University of Michigan Museum of Paleontology
USGS	United States Geological Survey
USNM	United States National Museum
UW	University of Wyoming
YPM-PU	Yale Peabody Museum Princeton Collection

Abbreviations of species names

A.g.	<i>Arapahovius gazini</i>
C.d.	<i>Carpolestes dubius</i>
C.e.	<i>Cantius eppsi</i>
C.h.	<i>Carpodaptes hazelae</i>
L.c.	<i>Lemur catta</i>
L.t.	<i>Loris tardigradus</i>
N.c.	<i>Nycticebus coucang</i>
Noth.	<i>Notharctus</i> sp.
O.c.	<i>Otolemur crassicaudatus</i>
P.c.	<i>Plesiadapis churchilli</i>
P.f.	<i>Plesiadapis fordinatus</i>
Ph.p.	<i>Phenacolemur praecox</i>
Pl.p.	<i>Plesiolestes problematicus</i>
S.g.	<i>Smilodectes gracilis</i>
T.g.	<i>Tupaia glis</i>
T.m.	<i>Tetonius matthewi</i>
T.s.	<i>Tarsius spectrum</i>

Chapter 1: Introduction

1.1 Statement of purpose

This study explores several issues related to feeding behaviour in the earliest primates and it suggests mechanisms of food breakdown they might have used. Based on the results of a unique experiment, I venture hypotheses about dietary preferences in the earliest primates.

Feeding behaviour is a broad topic with many components, but this study focuses on the physical (rather than psychological or social) processes involved in feeding behaviour. Therefore, the following four-step process can be called the ‘feeding process’. When a mammal feeds, it must find food that it recognizes *as* food (foraging), choose an individual food item from its environment and transport that item into its mouth (selection), then it must – if it is like most mammals – break that food item into fragments to allow a greater surface area for the chemical action of its digestive enzymes (breakdown). Finally, the food item must be processed chemically so that its nutrients might be assimilated into the mammal’s tissues (digestion). The focus of this study is step three, breakdown.

A mammal’s diet is the sum of all the foods it eats. Therefore an understanding of the feeding process is integral to an understanding of diet. For example, we humans choose not to include steel in our diet because we cannot digest it effectively (digestion). Equally, even if we could digest steel, it would not become part of the human diet because we are unable to chew it (breakdown).

There is some evidence of how extinct mammals found their food (foraging); for example, a mammal with large eyes and a reduced snout likely found its food by sight rather than by olfaction. The presence of prehensile limbs or prehensile anterior teeth suggests a particular mode of food selection and the exceptional preservation of stomach contents may indicate something about digestion. This study focuses on the food breakdown¹. Post-canine teeth (i.e., teeth that lie posterior to the canines) are very

¹ Also referred to as fragmentation. This is the act of reducing large items of food to small fragments of food.

powerful tools for studying food breakdown; they are thought to be adapted specifically for breaking food into smaller fragments. Fortunately, the mammalian fossil record is well-represented by premolar and molar teeth.

All components of feeding behaviour in living mammals can be studied either directly or indirectly. However, it is *necessary* to use indirect methods to study extinct mammals. Why is it desirable to understand feeding behaviour and diet in extinct mammals? An understanding of diet and feeding behaviour is indispensable to the establishment of a clear picture of past ecosystems and mammal biology. Dietary information can also have evolutionary implications; two groups of closely related mammals, each eating a different kind of food, may diverge morphologically, and may even become separate species.

This study is an attempt to answer the following questions:

1. What role do the different shapes of various primate dentitions play in breaking down different kinds of food?
2. How well do various measurements of dental features predict the effectiveness of certain teeth in breaking down different kinds of food? What can be said about the value of these measurements (i.e., how do the measurements ‘measure-up’)?
3. Can we suggest possible diets for some extinct primates based on their performances in a food breakdown experiment?
4. What can we learn about food breakdown mechanisms and mastication in primates from this experiment?
5. How should we characterize the evolution and especially the initial radiation of primates based on the answers to the above questions?

1.2 Diet in extant primates

At first glance, diet is a simple concept. Diet is that which an animal eats. However, some mammals eat many different kinds of food. Although it is easy to categorize lions as carnivores because they eat meat and cows are herbivores because

they eat plants, the issue becomes more complex with dietary generalists, like many primates. The following is a description of the diet of the slow loris, *Nycticebus*:

"Insects, fruit, leaves, seeds, birds, lizards, birds' eggs." (Napier and Napier, 1967, p. 234).

We might want to refer to this primate as an omnivore; however, many primates eat tree exudates (gums) even though this one does not. So if we call *Nycticebus* an omnivore, we might confuse others into thinking that the slow loris also consumes tree exudates. We might want to call *Nycticebus* an insectivore because it consumes more insects than anything else. However, its cousin, the slender loris (*Loris tardigradus*) also consumes more insects than anything else, *but* does not eat fruit.

Only recently (Strait 1993, 1997) have we begun to see the need for more precise, preferably quantifiable, dietary categories. Our concept of diet must also exclude cases of mammals consuming 'food' for purposes other than nutrition (e.g., chimpanzees consuming leaves for medicinal purposes, carnivores consuming plants for digestive cleansing) - though nutrition may be derived as a biproduct in some cases.

Compared to other mammalian orders, Primates is made up of dietary generalists. Some species are quite specialized, such as the aye-aye and the uakari (Napier and Napier, 1967; Ayres, 1998), but most are free to draw their nutritional requirements from various sources. Most primates are anatomically equipped to process many different kinds of food. Many live in the tropical rain forests where abundant, varied food sources are available.

1.3 Diet in extinct primates

The diet and the anatomy of a primate species influence one another reciprocally through evolutionary time. Some of the best evidence of this is in the morphology of the post-canine teeth. Long before Aristotle (translated by Peck, 1937), people have known that certain features are present in the molars and premolars of mammalian carnivores that are not present in mammalian herbivores (and vice versa). Features like these can be used to infer the diet of a mammal from its teeth alone. This process is reliable when the dental features are mutually exclusive and the diets are strikingly different. When more

precise dietary distinctions are required, the correspondent morphological features are more subtle and usually less reliable.

Assuming physical principles, such as those governing food breakdown, were the same in the distant past as they are today, tooth measurements that allow us to reliably infer diet in *extant* primates should apply equally to *extinct* ones. There are, of course, complications. Some extinct primates possess unique dental features. Examples include the plagioulacoid complex in carpolestids and the unique, highly basined molars of picrodontids. Relatively speaking, primates are dietary generalists with correspondingly generalized dentitions. Therefore, subtle features are necessary to separate primate species into different dietary categories. This subject will be treated in greater detail in Chapter four.

It is necessary to clarify how the term ‘primate’ is used here. Currently, the definition (i.e., taxa included) and the diagnosis (i.e., anatomical features necessary for inclusion) of Primates are much debated. There is some consensus as to what extant species should be included: most would now say that tree shrews are not primates, though this is a recent development. Plesiadapiformes is a group of mammals from the Paleocene and Eocene of North America and Europe. The taxonomic status of this group is uncertain. Because of dental features shared by plesiadapiforms and living primates, earlier researchers (e.g., Le Gros Clark, 1959) considered them to be a suborder of Primates. Now they are recognized to be quite different from living primates based on cranial and post-cranial features. In fact, plesiadapiforms may be more closely related to dermopterans (flying lemurs or colugos) than they are to primates (e.g., Beard, 1990). Furthermore, there is disagreement as to what families of Early Tertiary mammals should be included within Plesiadapiformes. Problems with the plesiadapiforms aside, the Eocene to Miocene adapoids and the Eocene to Oligocene omomyoids are widely held to be true primates.

For the purpose of this thesis, Plesiadapiformes is considered a suborder of the order Primates. The family Microsyopidae is treated as a part of the suborder Plesiadapiformes, following in this matter (and most other matters taxonomic) the classification in Fleagle (1999). This thesis is not a debate about the taxonomy of

primates. Conclusions that emerge from this study may have taxonomic implications, but those will be discussed in later chapters.

1.4 The mechanism of mastication in primates

In primates, the muscles responsible for chewing are much like those in generalized eutherians. Mastication is accomplished by the action of the temporalis, masseter, pterygoideus and digastricus muscle groups. The specific actions of these muscles in primates, as well as their anatomical peculiarities and relative strengths are detailed in Chapter 5.

Very little can be known about mastication in extinct primates. Some paleontologists have attempted to reconstruct muscle vectors in the masticatory apparatus of extinct primates (e.g., Gingerich, 1972). To do so, requires that the attachment sites for muscles and the temporomandibular joint elements be preserved, but most Paleocene and Eocene primates are known from teeth and jaws alone. Therefore, to simulate mastication in extinct primates, it is necessary to rely on modern analogues.

The question of what modern analogue to use for the earliest primates is a difficult one. Several have been suggested, from tree shrews (e.g., Goode and Haines, 1975) to lemurs (e.g., Fleagle, 1999). The most useful analogue is the thick-tailed bushbaby or galago, *Otolemur crassicaudatus*. This species is relatively primitive with respect to both feeding habits and morphology (Charles-Dominique, 1977; Rasmussen and Nekaris, 1998). Furthermore, the muscles of mastication and masticatory movements are well-studied in *O. crassicaudatus*. Mastication in no other mammalian species is as well-studied, with the exception of *Homo sapiens*. Therefore, the thick-tailed bushbaby is by far the best analogue to use to recreate mastication in the earliest primates.

Mastication speeds and directions as well as the total force generated by biting are well-documented in *O. crassicaudatus* (Hiiemae and Kay, 1973; Hylander, 1979). Prior to this study, the relative forces generated by the muscles of mastication in *O. crassicaudatus* were unmeasured. Accordingly, I measured the physiological cross sectional area in the masticatory muscles of this and closely related species. Physiological cross sectional area (or PCS) is an estimate of the cross sectional area of a

muscle and it is measured by dividing the weight of a muscle by the mean length of its constituent fibres (see also Chapter 5). PCS is considered a proxy for the strength of a muscle (e.g., Schwartz and Huelke, 1963). The results of this study were used to provide simulated masticatory muscles with realistic relative strengths. Details of my examination of the masticatory muscles of bushbabies are provided in Chapter 5.

1.5 Dental measurements used to infer diet

Most studies of diet in extinct primates do not actually test fossil teeth on real food. Instead, they rely on dental morphology to provide clues as to the dietary preference of the animal. Fossil teeth are compared to the teeth of living animals, and similarity in tooth morphology (especially molars and premolars) is thought to parallel similarity in diet. This sort of inference relies on a tight relationship between easily measured dental characteristics and dietary preference. Furthermore, it depends on the existence of a living species that has a similar dental morphology to the extinct species examined. No such living examples exist for the plesiadapiform carpolestids, picodontids or saxonellids, for example, and no good examples exist for the plesiadapiforms in general. An examination of the effect of various tooth morphologies on actual food is worthwhile. The most realistic way to accomplish this (apart from fitting small mammals with various different dentures) is *in vitro*, in a chewing simulation. Simulated chewing can be controlled with respect to variables, such as relative muscle force, chewing speed and the number of chewing cycles per test.

Several dental measurements are used to infer diet in extinct primates. Of these, three techniques were chosen. I assessed the predictive accuracy of these methods with reference to experimental masticatory performances². To do so, I used each technique to measure various dental specimens. These specimens were then used in the chewing experiment. I compared the results of measuring techniques to the results of the experiment to see if the measuring techniques accurately predicted chewing performances. The three morphometric techniques I used are explained in Chapter 4.

² ‘Masticatory performance’ refers to the size distribution of chewed fragments of food given a constant number of chewing cycles (Bates *et al.*, 1976).

They are from Seligsohn (1977), Kay (1975) and Evans and Sanson (1998). Chapter 8 examines the correlations between these techniques and chewing performances.

1.6 The fragmentation of food

Chewing (or mastication) is the primary action of the molar and, to a variable degree, premolar teeth of mammals. The function or *biological role* of mastication is the fragmentation of food into smaller parts (e.g., Hladik, 1979). Fragments of food are easier to digest than the entire original bite of food because they have more surface area for the same volume. Furthermore, a small fragment is easier to digest than a large fragment of the same shape because its surface area is greater relative to its volume. For instance, a cube 1 cm long has a surface area of 6 cm^2 ($1 \text{ cm} \times 1\text{cm} \times 6$ sides) and a volume of 1 cm^3 ($1 \text{ cm} \times 1\text{cm} \times 1\text{cm}$) for a surface area: volume ratio of 6:1. A cube 2 cm long has a surface area of 24 cm^2 ($2 \text{ cm} \times 2\text{cm} \times 6$ sides) and a volume of 8 cm^3 ($2 \text{ cm} \times 2\text{cm} \times 2\text{cm}$) for a ratio of 24:8 or 3:1.

In this study, the relative mastication (or trituration) proficiencies of various species given various kinds of food are assessed. Given the above assumption about the function of mastication, masticatory proficiency is equivalent to the effectiveness of a particular species at fragmenting a particular food. Because small fragments are easier to digest, the more smaller fragments that are produced by mastication, the more effective the mastication. I measured the increase - due to mastication - in the surface area to volume ratio of food. This was accomplished by comparing this ratio in the pre-mastication food sample to the ratio in the post-mastication food fragments. Further discussion of this method is in Chapters 7 and 8.

1.7 Simulated mastication

I built a machine that simulates mastication. This machine reproduces the forces that occur during mastication in the thick-tailed bushbaby, *Otolemur crassicaudatus*. Seven pairs of muscles are simulated by seven pairs of steel cables. These cables act in roughly natural orientations with roughly natural magnitudes of pull. They exert their

force upon an epoxy mandible that was cast from the mandible of a thick-tailed bushbaby. Muscle cables are cemented to the mandible at natural points of insertion. The mandible is cemented to an epoxy skull (from the same individual) at the mandibular condyle. The occlusal surfaces of the mandible and skull are sanded flat, such that prosthetic dentitions may be attached and removed easily. The machine is driven by an electric motor and the chewing action is driven by the rotation of cams (one per muscle) in an overhead assembly. Cams are configured such that each muscle acts at the proper time with the proper duration. Construction details for this machine are in Chapter 6.

Casts of upper and lower tooth rows (P3-M3 and p3-m3) belonging to different species can be inserted into this machine. It was necessary to choose fossil specimens that occlude well and that belong to the same species - though the latter is never certain unless they belong to the same individual. Tooth rows also had to fit onto the jaws of the skull.

Once a dentition was in place, it was tested on fourteen different kinds of food, five samples each. Ten full chewing cycles were enacted for each food sample, at the end of which food fragments were passed through a column of sieves. The contents of each sieve were emptied and weighed to generate measures of the effectiveness of fragmentation for each species-food pair (see Chapters 7 and 8 for further methodological details). These results can be used to generate dietary inferences and they can be compared to various morphometric techniques to assess the realism of dietary inferences made using dental morphometrics.

1.8 Experimental design

The focus of this study is a ‘paleontological experiment’. The following key elucidates the logical framework of this experiment. It is much like those keys used to identify extant mammals.

- 1. Null hypothesis: all dentitions will fragment all food equally effectively in the chewing experiment.
 - If the null hypothesis is true, then end experiment (inconclusive results).

2. Hypothesis 1: different dentitions will fragment each kind of food with differential success.
 - If hypothesis 1 is true, then go to B.
- B. 1. Null hypothesis: food fragmentation performances will not correlate to Seligsohn's diet-related tooth measurements (see Chapter 4).
 - If the null hypothesis is true, then the usefulness of Seligsohn's method for inferring diet is in doubt.
2. Hypothesis 1: food fragmentation performances *will* correlate to Seligsohn's diet-related tooth measurements.
 - If hypothesis 1 is true, then the usefulness of Seligsohn's method is vindicated.
- C. 1. Null hypothesis: food fragmentation performances will not correlate to tip sharpness and cusp sharpness.
 - If the null hypothesis is true, then the usefulness of Evans and Sanson's method for inferring diet (see Chapter 4) is in doubt.
2. Hypothesis 1: food fragmentation performances *will* correlate to tip sharpness and cusp sharpness.
 - If hypothesis 1 is true, then the usefulness of Evans and Sanson's method is vindicated.
- D. 1. Null hypothesis: food fragmentation performances will not correlate to Kay's diet-related tooth measurements (see Chapter 4).
 - If the null hypothesis is true, then the usefulness of Kay's method for inferring diet is in doubt.
2. Hypothesis 1: food fragmentation performances *will* correlate to Kay's diet-related tooth measurements.
 - If hypothesis 1 is true, then the usefulness of Kay's method is vindicated.

It is possible to assess the usefulness and predictive power of my own experiment with reference to the above framework. Significance tests were used to assess hypothesis A and tests of correlation were used to assess hypotheses B, C and D. These statistical tests and attendant assessments are in Chapters 8 and 9 respectively.

My simulation of mastication is a *simplified* version of a very complex behaviour. It uses a *single* extant species to model mastication, while testing dentitions from *several* species. Clearly I have done this to isolate the variable of premolar+molar morphology, but masticatory differences surely exist among the various species tested. This study is far from providing the final word on diet in the earliest primates. Nevertheless, it describes a new method to infer diet and offers a unique contribution to this field.

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Chapter 2: The earliest primates

2.1 Introduction to plesiadapiforms and early euprimates

Before investigating the paleobiology of the earliest primates, it is necessary to decide what taxa belong in the order Primates and what characters can be used to admit new fossil taxa when they are discovered. Both the definition¹ (i.e., the taxa included) and the diagnosis (i.e., the characters requisite for inclusion) of Primates are matters of contention. The general consensus among primatologists is that there is no single character that can be used to diagnose Primates (Le Gros Clark, 1959; Martin, 1968; Gingerich, 1984; Conroy, 1990). Rather, most primatologists attempt to diagnose the order using a suite of characters or trends (Mivart, 1873; Le Gros Clark, 1959; Martin, 1968).

The earliest definition of the order Primates was given by Linnaeus in the tenth edition of his *Systema Naturae* (Conroy, 1990). He included bats, flying lemurs and all the known extant primates (defined as they are today). He diagnosed Primates on the possession of four characters: four incisors at the front of the upper jaw, two clavicles, two mammae and at least two grasping extremities. Clearly, the members of the group under diagnosis and the characters used in the diagnosis are inseparable. Several groups of mammals possess four upper incisors and several possess two clavicles. Some primates possess more than two mammae (Martin, 1968), and some non-primate mammals possess at least two grasping extremities (e.g., the marsupial koala).

The most widely quoted diagnosis of the Primates comes from Mivart (1873):

“Unguiculate clavicate placental mammals, with orbits encircled by bone; three kinds of teeth, at least at one time of life; brain always with a posterior lobe and calcarine fissure; the innermost digits of at least one pair of extremities opposable; hallux with a flat nail or none; a well-developed caecum; penis pendulous; testes scrotal; always two pectoral mammae” (Mivart, 1873, p. 507).

Mivart’s diagnosis owes a great deal to that of Linnaeus and suffers from the same criticisms. Many of these features (e.g., possession of clavicles) are shared-primitive characters of placentals. Many arose independently in several placental lineages (e.g., post-orbital bars). Regardless of the cladistic unacceptability of Mivart’s diagnosis, it is difficult to apply it to fossil primates as most characters refer to soft tissue anatomy. However,

Mivart's *definition* of Primates resembles modern ones in the exclusion of bats and colugos.¹

Le Gros Clark (1959) suggested that primates are mainly distinguished from other orders of placental mammals based on their lack of specialization. His attempt to diagnose Primates consists of a set of general trends. They can be summarized as follows (see also Le Gros Clark, 1959, p. 43):

1. retention of pentadactyl and primitive limb elements (e.g., clavicles)
2. enhanced digital mobility, of especially the pollux and hallux
3. flattened nails and tactile digit pads rather than claws
4. reduction in the olfactory apparatus and the length of the snout
5. elaboration of the visual apparatus; sometimes binocular vision
6. loss of some teeth but retention of a simple molar cusp pattern
7. large, elaborate brain, especially the cerebral cortex
8. elaborate, efficient mechanisms for prenatal nourishment

All but the last trait are detectable in the fossil record of primates. Martin (1968) argues that the validity of this diagnosis depends on a clear understanding of the condition of all the above traits in the non-primate eutherian that gave rise to primates. This condition, although perhaps better known today than in 1968, is a matter of conjecture.

Le Gros Clark's definition of primates, echoed later by Simpson (1945), included tree shrews (Superfamily Tupaioidea), despite earlier work that very strongly suggested affinities between tree shrews and elephant shrews (Evans, 1942). Currently, tree shrews are thought to constitute their own order, the Scandentia (Van Valen, 1965; Goodman, 1975; McKenna, 1975; Butler, 1980; Luckett, 1980; Wible and Martin, 1993). The characters once used to include tree shrews within the order Primates are now thought to be mainly shared primitive characters or incidences of convergence (see especially Van Valen, 1965).

More recently, primates have been characterized by patterns in the basicranium. Szalay (1975; Szalay and Delson, 1979) characterizes the primate basicranium as follows (Szalay and Delson, 1979, p. 26):

1. Bulla formed by the petrosal bone
2. Partly extrabullar or intrabullar ectotympanic bone
3. Medial internal carotid artery is lost
4. Promontorium of the petrosal is rounded
5. The entire intrabullar carotid circulation is encased in bone

¹ Here, 'definition' is equivalent to 'taxonomic content'.

6. The fenestra rotunda is ventrally shielded by the internal carotid canal

This diagnosis is apparently well-accepted (MacPhee *et al.*, 1983; Conroy, 1990), and because these characters are based on the cranium, it can be applied to the fossil record. However, each of these features (except perhaps the petrosal bulla) is present in other mammalian orders (Martin, 1990). Furthermore, there is a great deal of variation in extant primates with respect to these features, especially in the pattern of carotid circulation.

Elsewhere, Szalay suggests the use of exclusively dental characters to distinguish primates from non-primates. He suggests that the molar cusps are reduced and bulbous, the trigonid is low relative to the talonid (as compared to non-primate ‘insectivorans’), and that the conules on the upper molars are large (Szalay, 1968a, p. 29). Dental characters have a wider application in primate paleontology because most early fossil primates are known from teeth alone. However, a dental diagnosis lacks precision in this case, as several Paleocene eutherians possess molars with low, bulbous cusps, low trigonids and large conules (e.g., several condylarths).

The choice of characters to diagnose Primates depends on the taxa that are included in Primates (and vice-versa). The features used by Linnaeus, Mivart, Le Gros Clark, Szalay and others reflect their ideas about the inclusiveness of the order Primates. To include tree shrews, for example, in the order Primates, it is necessary to choose diagnostic characters that tree shrews and primates share.

Currently, the debate over the ordinal status of Plesiadapiformes has a profound influence on the characters used to diagnose Primates. Some (e.g., Szalay, 1968a; Gingerich, 1984; Covert, 1986) consider plesiadapiforms, at least in part, to be primates - albeit the most primitive primates. Others (e.g., Cartmill, 1972; Beard, 1990; Martin, 1990) exclude plesiadapiforms from the order. The rationale for including plesiadapiforms within the order Primates, as well as the rationale for excluding them, are presented in the following section.

2.2 The status of plesiadapiforms

The ‘archaic primates’ of the Paleocene and Eocene (and perhaps the latest Cretaceous) have been classified in various different ways. Today, they are usually grouped within a single suborder Plesiadapiformes (e.g., Conroy, 1990; Fleagle, 1999), within the order Primates.

The Plesiadapiformes includes at least four families: the Plesiadapidae, Paromomyidae, Carpolestidae and Picrodontidae (Martin, 1990). The Saxonellidae is

nearly always included. The Microsyopidae is sometimes included (e.g., Gunnell, 1989; Fleagle, 1999) but it is often excluded (e.g., Szalay and Delson, 1979) based on the morphology of the basicranium. Microsyopids do not have a definite petrosal bulla. The bullar region is preserved in *Microsyops latidens*, but no ossified bulla is present. Gunnell (1989) suggests that the bulla may have been cartilaginous or absent, and that a cartilaginous bulla may be primitive for plesiadapiforms in general - a primitive retention in microsyopids. Furthermore, several features of the lower molars in microsyopids (e.g., twinned entoconid-hypoconulid) are thought by Szalay (Szalay and Delson, 1979) to ally this family with mixodectids (an extinct family of insectivorans with uncertain affinities) instead. This is not a clear-cut difference of opinion, however. Szalay removes a number of genera from the Microsyopidae (*sensu* Bown and Gingerich, 1973; Rose, 1981; Gunnell, 1989; Fleagle, 1999) and places them into the Paromomyidae, a family he admits to the order Primates. Some of these are *Plesiolestes*, *Palaechthon*, *Navajovius* and *Palenochtha* (compare Szalay and Delson, 1979 to Fleagle, 1999).

Plesiadapiforms for which the cranium or post-cranium is known fail to possess several features diagnostic of Primates. *Plesiadapis* is known from skeletal material and possesses claws rather than flattened nails, and the first digit was not especially opposable (Conroy, 1990). Moreover, all known plesiadapiform crania fail to possess a post-orbital bar and the orbits tend to face laterally (Martin, 1990). Though *Plesiadapis* possesses an ectotympanic ring enclosed within the bulla (Gingerich, 1976), the bulla is not necessarily formed by the petrosal. Though it is continuous with the petrosal, no suture is visible. As mentioned, *Microsyops latidens* shows no evidence of an ossified bulla, and yet the petrosal bone is present (Gunnell, 1989). This species also lacks a post-orbital bar. The skull of *Palaechthon nacimenti* possesses features that suggest vision in this species was poorly developed relative to extant primates, and that olfaction was strongly developed (Kay and Cartmill, 1977). A skull of *Ignacius graybullianus*, with a well-preserved basicranial region, was described by Kay *et al.* (1992). The basicranium of this skull reveals a clear suture between the bone flooring the auditory bulla and the adjoining petrosal bone. Kay *et al.* suggested that in this species, the bulla is formed by the entotympanic. However, this feature does not support a special relationship between *Ignacius* and dermopterans because most of the bulla in *Cynocephalus* is formed by the ectotympanic bone (see Fox, 1993).

The above facts suggest that Szalay and Delson's (1979) diagnosis of Primates is inconsistent with the inclusion of some species of plesiadapiforms in the order. Conversely, Szalay (1972a) described a crushed cranium of *Phenacolemur jepseni* that possesses an auditory bulla composed of the petrosal bone. If some plesiadapiforms possessed a petrosal bulla, and others did not, perhaps this feature is not primitive for Plesiadapiformes.

As more non-petrosal plesiadapiform bullae are discovered, the probability that they possessed petrosal bullae becomes vanishingly small.

The primate status of plesiadapiforms has been attacked on other grounds. Based on the disarticulated material of *Phenacolemur* and *Ignacius*, Beard (1989, 1990) suggested that the phalanges of paromomyids closely resemble those of extant dermopterans. He further suggested that these resemblances (long, thin intermediate phalanges, circular in cross-section) were functionally linked and that the paromomyids represent the first incidence of a gliding habitus in mammalian evolution (Beard, 1989). Although this suggestion has gained support because of resemblances between the cranium of *Ignacius graybullianus* and that of *Cynocephalus* (Dermoptera) (Kay *et al.*, 1990; Kay *et al.*, 1992), it has also been criticized. Krause (1991) pointed out the disarticulated condition of the specimens in Beard's analysis. He suggested there is no way to be certain whether the phalanges are intermediate or distal, or even whether they belong to the manus or the pes. Hamrick *et al.* (1999) performed a detailed analysis on the proximal and intermediate phalanges of *I. graybullianus* and several other mammals including *Cynocephalus*, rodents and prosimians. They concluded that the putatively intermediate phalanges of the paromomyid resemble those of the dermopteran, but that they also resemble those of the squirrel *Anomalurus*, and that they resemble most of all the *pedal* phalanges of *Cynocephalus*. A close phylogenetic relationship between paromomyids and dermopterans is not ruled out, but the suggested functional adaptation of paromomyid phalanges is for "vertical clinging and climbing on large-diameter arboreal supports" (Hamrick *et al.*, 1999, p. 397). Moreover, Runestad and Ruff (1995) investigated the limb proportions of paromomyids and found that the distal segments were short compared to those in extant mammalian gliders. Perhaps then, similarities between plesiadapiform limb elements and those of many non-primate mammals are functional similarities without necessary phylogenetic implications. This controversy is unresolved.

Recently, three new families have been added to the Plesiadapiformes. *Micromomyidae* was erected to include the formerly microsyopid (*sensu* Fleagle, 1988) genera *Micromomys* and *Tinimomys*. Rose and Bown (1996) erected the family *Picromomyidae* to include a new genus *Picromomys* and a former microsyopid (*sensu* Fleagle, 1988). Most recently, Hooker *et al.* (1998) erected the family *Toliapinidae* to include a new genus, *Toliapina*, two former microsyopids, *Berruvius* and *Avenius*, and the contentious African genus, *Altiatlasius* (Sigé *et al.*, 1990).

Each of the above views on the status of the plesiadapiforms has its merits. The status of the Plesiadapiformes and the interrelationships within this group are of secondary importance here, but it is necessary to use taxonomy here for the purposes of effective

communication. To this end, I will adhere to the classification presented in Fleagle, 1999. This is perhaps the most inclusive alternative. Furthermore, it has the advantage of being recent and including the majority of the taxa known or suspected to be plesiadapiforms.

Though it is now fashionable (e.g., Kay *et al.*, 1992) to exclude the plesiadapiforms from the Primates, this may prove disadvantageous in the long run. The similarities between so called ‘archaic primates’ and ‘true primates’ are useful for shedding light on the adaptive origins of primates. Equally, the differences help us to understand the environmental pressures on primates during the late Paleocene and early Eocene transition that gave rise to primates of modern aspect. Most evidence suggests that the Plesiadapiformes are the closest sister group to Primates, if they are not Primates themselves. If this relationship is accepted, then whether one considers plesiadapiforms to be primates or not becomes a matter of taste. Should the nonprimate-primate boundary be drawn between plesiadapiforms and their nonprimate eutherian ancestors or should it be drawn between plesiadapiforms and euprimates? Though we have no evidence of the nonplesiadapiform ancestors of plesiadapiforms, the former approach would leave us with an evolving suite of primates from the latest Cretaceous to the present. This is a convenient group for the study of paleobiological changes during the Tertiary; therefore, I favour the inclusion of the plesiadapiforms within the order Primates. Furthermore, for those studying the evolution of euprimates *and* plesiadapiforms, it is expedient to use a single ordinal term for both groups.

In accordance with the classification given in Fleagle (1999), the plesiadapiform taxa included in this study are the following:

Suborder Plesiadapiformes

Family Plesiadapidae

Plesiadapis churchillii

Plesiadapis fordinatus

Family Carpolestidae

Carpodaptes hazelae

Carpolestes dubius

Family Paromomyidae

Phenacolemur praecox

Family Palaechthonidae

Plesiolestes problematicus

From among the appropriate² specimens at my disposal, I chose specimens representing species from as many different families as possible. Unfortunately, no appropriate saxonellids, picodontids, picromomyids or toliapinids were available to me. Some specimens of *Micromomys* and *Tinimomys* (Micromomyidae) were available; however, the *Micromomys* specimens were too fragile to cast safely, and *Tinimomys* is so small that the casts made from it failed to set properly.

2.3 The earliest ‘true primates’

The term *euprimate*, meaning ‘true primate’, was coined by Simons (1972) to describe a group of primates that appear initially in the earliest Eocene. They are primarily North American and European and are usually classified in two families: the Adapidae and the Omomyidae. Neither family has extant representatives.

2.3.1 Adapidae

The Adapidae are divided into two subfamilies: the Notharctinae, all from the Eocene of North America; and the Adapinae, all but one species from the Eocene and Oligocene of Europe and Asia. One adapine species, *Mahgarita stevensi*, is known from the late Eocene of Texas.

The adapids may be closely related to extant and subfossil lemurs. Similarities are not only dental, but also cranial and post-cranial; several species are known from nearly complete skeletons (e.g., *Notharctus tenebrosus* and *Smilodectes gracilis*). Szalay and Delson (1979) and Fleagle (1999) place the family Adapidae within the infraorder Lemuriformes to reflect this relationship. Perhaps the greatest testament to this relationship is Gregory’s 1920 monograph on *Notharctus* (Gregory, 1920).

One of the main reasons for the inclusion of plesiadapiforms in the order Primates is the similarity between the molars of some plesiadapids and primitive notharctines (e.g., Simpson, 1935), especially *Cantius*. However, a recently discovered cranium of *Cantius abditus* resembles extant lemurids with respect to the carotid circulation in the ear region (Rose *et al.*, 1999).

All diagnostic skeletal characters of adapids suggest that they are primates.

² That is, those having the five posterior-most teeth, for which there is an occluding specimen from the same side.

I tested three adapid species in this study. They are the following (classification as in Fleagle, 1999):

Infraorder Lemuriformes

Family Adapidae

Subfamily Notharctinae

Cantius eppsi

*Notharctus sp.*³

Smilodectes gracilis

2.3.2 *Omomyidae*

The affinities of omomyids are unclear. In some respects they resemble extant tarsiers. This is especially apparent in three genera known from skulls: *Shoshonius*, *Tetonius* and *Rooneyia* (Gingerich, 1981; Beard *et al.*, 1991). Recently discovered crania of *Omomys* share some features with extant lorises (Alexander and MacPhee, 1999). Early paleontologists noted the similarities between omomyids and extant tarsiers (Jones, 1929). Shortly after its discovery, Cope (1885) noted the similarity of the omomyid *Tetonius homunculus* to tarsiers. Several authors ally omomyids with tarsiers in the infraorder Tarsiiformes (e.g., Gingerich, 1977; Szalay and Delson, 1979; Bown and Rose, 1987). Others (e.g., Covert and Williams, 1994) question the usefulness of this association; no known omomyid is thought to have had a similar adaptive profile to that of *Tarsius*.

Within the Omomyidae are three subfamilies. The Anaptomorphinae contains species that are all from the Eocene of North America and Europe. They are all relatively small and primitive (Fleagle, 1999). Only *Tetonius homunculus* is known from cranial material: a specimen with a badly damaged basicranium.

³ The status of this genus is in flux (e.g., Gunnell, 1999). Godinot (1998) suggests “a complete reappraisal of notharctine systematics and phylogeny is needed” (p.231). Without prior identification, I hesitate to assign test specimens of *Notharctus* to species. The mandible I used belongs to probably *N. venticulus* (*sensu* Krishtalka *et al.*, 1990) and the maxilla belongs to probably *N. tenebrosus* (*sensu* Godinot, 1998). The former may represent the ancestor of the latter: they intergrade morphologically (Godinot, 1998). Moreover, the two specimens occlude very well. I believe it justified, therefore, to use these two specimens together as if they belonged to a single species.

The omomyines are entirely North American and are known from the Eocene and the Oligocene. One species, *Rooneyia viejaensis*, is known from cranial material that suggests some affinity with tarsiers. However, the only known post-cranial material, belonging to *Hemiacodon gracilis*, shows adaptations to saltatory locomotion that are reminiscent of extant lemurs and galagos (Fleagle, 1999).

The Microchoerinae are purely European, known from the Eocene and Oligocene. Although it contains few species, this group is well-known anatomically. Several complete skulls of *Necrolemur* show resemblances to both tarsiers and lemurs, especially in the configuration of the bony support for the tympanic membrane, which appears to be an intermediate condition between that in lemurs and that in tarsiers (Cartmill, 1982 in Fleagle, 1999). The isolated post-cranial remains attributed to microchoerines appear to be adapted to saltatory locomotion (Schmid, 1979).

As with adapids, omomyids appear to possess all the diagnostic skeletal characters of primates.

I have tested the following species of omomyids (classification as in Fleagle, 1999):
Suborder Prosimii

Family Omomyidae

Subfamily Anaptomorphinae

*Tetonius matthewi*⁴

Subfamily Omomyinae

Arapahovius gazini

Specimen numbers for all species listed here are given in Appendix 1.

2.4 Biology of the earliest primates

Several groups of placental insectivores have successfully retained a primitive lifestyle since the Late Cretaceous (Vaughan, 1986). Why then did primates move away from this lifestyle? When did they undergo this adaptive shift⁵? What were the dietary and/or locomotor changes that accompanied this shift? Ultimately, we may discover that the

⁴ The mandibular tooth row used for this species is considered by Bown and Rose (1987, p. 57) to be a '*Tetonius matthewi - Pseudotetonius ambiguus* intermediate'.

⁵ Defined as a suite of interrelated morphological changes within a lineage as a response to a significant behavioural change, e.g., the change in a lineage from insectivory to herbivory (Cartmill, 1972). A particularly successful adaptive shift may result in an adaptive radiation.

primitive lifestyle for primates is *no different* from that of their nonprimate ancestors. In this case, the diversity of lifestyles and adaptations in extant primates have arisen independently in different primate groups. If so, the ordinal status of the Primates should be questioned. Assuming, conversely, that an adaptive shift took place at the nonprimate-primate boundary, the characterization of that shift is important to our understanding of Primates.

2.4.1 *The arboreal hypothesis*

Several primatologists have attempted to characterize the defining primate adaptive shift. The first published attempt to characterize the primates with reference to their primitive biology was that of Smith (1912), rapidly followed by that of Jones (1916). Both suggested that the distinguishing features of primates arose as adaptations to life in an arboreal milieu.

Grafton Elliot Smith was particularly concerned with the differences between sensory development in primates and that in insectivorans. He ventured that the elaboration of the visual, auditory and tactile senses in primates resulted from life in the trees (Smith, 1912). The loss of acute olfaction and shortening of the primitively long snout occurred as a result of leaving the forest floor, and the frontation of the orbits was simply a side-effect of snout retraction.

F. W. Jones, who was concerned primarily with post-cranial anatomy, suggested that the flexibility of primate limbs (though he considered these to be primitive retentions), as well as the tactile and opposable first digits, are adaptations to moving around in the branches of trees. Perhaps suffering from a lack of evidence, Jones conjectured that the primitive condition in mammals was arboreal (Cartmill, 1974). Further, he suggested that arboreality was attained in the ancestors of primates in the late Triassic.

A great deal of confusion has arisen from the Smith-Jones hypotheses of primate paleobiology (see for example, Cartmill, 1974; Raczkowski, 1975 and Cartmill's response; Shaklee, 1975 and Cartmill's response). Note that Smith and Jones defined the Primates rather inclusively: tree shrews, representing a variety of niches from entirely terrestrial to entirely arboreal, were included. Despite Smith's inclusive treatment of Primates, he was clear in suggesting that the shift in sensory development from primarily olfaction to primarily vision occurred at the transition from tupaioid forms to 'anaptomorphoid' or 'tarsioid' forms. Le Gros Clark (1959) essentially followed the ideas of Smith and Jones in his elaboration of the 'arboreal theory' of primate adaptation. He too included the tree shrews as primates.

Modern proponents of the arboreal theory of primate evolution include Szalay (1972b; Szalay and Delson, 1979) and to some degree Sussman (1991). Both suggest that, relative to their nonprimate ancestors, the earliest primates possessed herbivorous adaptations.

2.4.2 *The visual predation hypothesis*

Cartmill (1972, 1974) criticized the arboreal theory of primate evolution on several grounds. Doing so, he relied on Le Gros Clark's (1959, see above) suite of diagnostic primate features. Whereas many mammals are highly adapted to the arboreal niche, only primates have developed these features: forward-facing orbits encircled or encased by bone; opposable, grasping first digits; highly developed vision; loss of olfaction accompanied by retraction of the snout; and generally very large brains relative to body size. Tree squirrels are well-adapted to life in the trees, yet they possess compressed claws, non-opposable digits and relatively small brains. Despite their failure to possess the characteristic primate features (thought by Smith and Jones to constitute arboreal adaptations), squirrels are very agile and successful in the trees. Therefore something beyond simple arboreality must have driven the evolution of the earliest primates.

Cartmill suggested that the above primate characters evolved as adaptations to slow, careful predation on insects in slender, terminal branches in the forest understory. Mammals that possess opposable digits often use them to grasp insect prey. Some examples are arboreal mice and rats, South American opossums and some diprotodont possums. Cartmill also noted that chameleons use their grasping extremities for predation on insects (Cartmill, 1974). Conversely, chameleons have significantly *divergent* orbits and many marsupials that possess grasping, opposable digits are entirely herbivorous (e.g., koalas).

Cartmill compared the orbital morphology of primates to that of owls and cats. Owls and cats are highly predaceous and possess markedly convergent orbits. The overlap in visual fields allowed by orbital convergence confers excellent depth perception - useful in gauging the distance to moving prey. Primates possess convergent orbits and opposable, grasping digits. By analogy, Cartmill suggested that the first primates were adapted to a predatory lifestyle.

Cartmill also attempted to fit the flattened nails of primates into this story. Many arboreal animals possess claws. These claws are useful for clinging to large trunks: they dig into the bark while the animal's paw is splayed. However, when the branch in question is narrower than the splayed paw, the claws fail to make contact with the substrate. In such

a situation, a prehensile digit that can curl around the narrow branch is ideal. Preferably that digit possesses a fleshy pad on its under surface with sufficient relief to grip the smooth bark of a young branch and preferably there is no claw with which to stab oneself whilst curling one digit over an opposing digit. Most primates (*Daubentonina* is an exception) possess clawless prehensile digits with tactile pads (Cartmill, 1972, 1974).

The visual predation hypothesis of primate evolution was well received. For a long time, arguments against it were few and generally flawed (see the responses to Cartmill, 1974, by Raczkowski (1975) and Shakalee (1975)). Despite flaws of its own, the visual predation theory went virtually unchallenged for two decades.

Potential problems with this hypothesis may result from poor analogies between primates and other animals. No other animal possesses the entire suite of characters Cartmill used to diagnose primates. Therefore, he can only draw parallels with respect to one or a few traits. For example, cats possess binocular vision, yet they did not evolve large brain size or opposable thumbs. Another problem stems from the fossil record. Cartmill excluded the herbivorously adapted plesiadapiforms from the order Primates to validate his hypothesis. However, the most primitive and earliest euprimates possess herbivorous dental adaptations. For example, *Cantius* is thought by most to be a frugivore and *Notharctus* and *Smilodectes* are thought to be frugivore-folivores (Covert, 1986). If the emergence of primates was characterized by a shift to preying on insects in the slender supports of trees, then primates rapidly shifted again toward a herbivorous existence. This point is particularly important as Cartmill accepted that the euprimates may have split from the plesiadapiforms as late as the mid-Paleocene. If this split happened as late as the middle of the Paleocene, then the adaptive shift towards arboreal-insect-predation and the subsequent shift to herbivory must have been rapid events indeed. Regardless, there is no evidence for either adaptive shift.

The oldest adapids and omomyids are from the early Eocene, approximately 53 million years ago (Gingerich, 1986). The oldest adapid genus is *Cantius*, probably a frugivore. Finally, the earliest adapids and omomyids resemble one another to such a great degree that many primatologists feel that the origin of the euprimates was as late as the late Paleocene (Fleagle, 1988).

2.4.3 *The angiosperm co-evolution hypothesis*

Based on his earlier work on ecological interactions between angiosperms and their dispersal agents, Sussman (1991) added a vital step to Cartmill's hypothesis. He suggested that Cartmill's analysis is flawed in several ways. The first flaw is the assumption that most

extant, primitive primates are adapted to insectivory. In fact, very few primates are primarily insectivorous. Those that are (e.g. tarsiers, some galagos, lorises) tend to use their senses of smell and hearing - not vision - when they hunt (Charles-Dominique, 1977). Despite their convergent orbits, cats also depend more on olfaction than on vision when tracking (Sussman, 1991). Furthermore, an arboreal marsupial, *Caluromys*, hunts insects using vision in the terminal branches of trees and possesses divergent orbits and claws (Rasmussen, 1990). However, this South American opossum also harvests fruit without the requisite primate-like adaptations.

Rather than hunting insects, Sussman ventured, primates were hunting fruit. He accepted (as I do) Cartmill's arguments about the functional significance of grasping, opposable, clawless digits, and kept the first primates on the terminal branches of trees. Sussman argued that the angiosperm radiation was in full swing by the early Paleocene and that flowering plants were diversifying at a steady rate throughout the epoch. Angiosperms during the Paleocene produced a number of nutritive structures: flowers, small, dry fruits, nectar, leaf buds and gums were probably all exploited by the plesiadapiforms (Tiffney, 1981). If, as Gingerich (1976) suggested, many of the plesiadapids were terrestrial herbivores, this must reflect a secondary derivation - plesiadapiforms were primitively arboreal. The earliest archaic primates were probably insectivores (Kay and Cartmill, 1977), but several herbivorous forms arose during the Paleocene (Szalay and Delson, 1979). Sussman suggested that this was a result of the continued diversification of the angiosperms and that primates, bats, frugivorous birds and flowering trees *co-evolved* throughout the early Tertiary. As frugivores became more proficient at harvesting fruit, angiosperms developed mechanisms to 1. protect their seeds (hence very small seeds that avoid being masticated and very large seeds that get dropped) and 2. attract potential dispersers (hence nutrient-rich fleshy fruit).

Sussman explained the visual acuity of primates as an adaptation to successfully locating, accessing and seizing fruit in the terminal branches of trees. Because the arboreal environment is complex and highly three-dimensional and because fruit is distributed in spatially separated patches, visual acuity and brain power are assets to arboreal frugivores. Furthermore, the dexterity of the primate hand is an adaptation to grasping fruit. If a fruit falls to the forest floor when plucked, the clumsy primate must either find another or risk predation to retrieve it.

At the end of the Paleocene, we begin to see the first truly fleshy fruits. These become common in the Eocene: most modern families of fruit-bearing angiosperms have appeared in the fossil record by this time (Wing and Tiffney, 1987). Perhaps it was the emergence of these fleshy fruits that allowed for the radiation of primates of modern aspect

(Sussman, 1991). If so, then one might predict that the first primate molars resembling those of extant primate frugivores would appear in the Eocene. This appears to be the case (e.g., Covert, 1986), but whether or not these early euprimates and/or the archaic primates before them were frugivores (as opposed to insectivores, folivores, etc.) is a question addressed by this study.

The angiosperm co-evolution hypothesis holds the greatest promise for explaining the initial radiations of primates in the Paleocene and Eocene. It combines the best aspects of the arboreal hypothesis and the visual predation hypothesis. Furthermore, it makes sense functionally as well as ecologically and it applies to both plesiadapiforms and euprimates. If it is true, then the primitive condition of plesiadapiforms is arboreal insectivory and that of euprimates is arboreal insectivory-frugivory. One should then extrapolate that those extant primates occupying an arboreal insectivorous-frugivorous niche (e.g., many species of galagids and cheirogaleids) either retain or have recaptured the primitive condition.

2.4.4 *Complications*

In his 1990 review of the three hypotheses (above), Rasmussen suggested that there is a significant degree of overlap between them. He studied the behaviour of the South American opossum *Caluromys derbianus*, which he suggested represents a morphological intermediate between plesiadapiforms and euprimates.

This marsupial possesses a relatively large brain and orbits, reduced claws and tactile digital pads, a large post-orbital process and small litters with reduced (for marsupials) rates of development (Rasmussen, 1990). *Caluromys* is highly arboreal, spends most of its time in the terminal branches of trees, but it is both insectivorous *and* frugivorous. Rasmussen suggested that, by analogy to this opossum, the earliest primates were adapted to visual predation on insects *and* fruit in the terminal branches of trees. He further suggested that this trend began with the plesiadapiforms that were typical arboreal insectivores primitively, but they developed herbivorous dental adaptations over time. Next, euprimates emerged. These were adapted to frugivory in the terminal branches of trees primitively, but they shifted to catching insects over time. This series of positional and dietary influences shaped the characteristic morphology of the earliest primates. One flaw in this argument is that the very animal upon which he bases his analogy fails to possess true post-orbital bars, flattened nails and orbital convergence.

The consumption of tree exudates may have played a significant role in the early evolution of primates. Tree gum is a large component of the diet of many small primates

(Bearder and Martin, 1980; Nash, 1989; Ferrari, 1998). Gum is a viscous liquid secreted by certain trees in response to the activity of wood-boring insects. It is neither sap nor resin - it has a different chemical composition and physical properties. Bearder and Martin (1980) defined it as

“a group of amorphous, acidic polysaccharides of complex and variable chemical and structural composition. Gums are entirely soluble in water or soften to form a thick glutinous liquid or mucilage” (p. 105).

To digest gum, most gummivorous primates likely host special gum-fermenting bacteria (Bearder and Martin, 1980; Nash, 1989). Based on the shared presence of fermenting bacteria in the gut, Nash suggested that the gum-fermenting condition is similar to the condition in cellulose-fermenting folivorous primates. Nash further suggested that if the earliest primates were not only insectivores, but also specialized gummivores, those primates could easily have given rise to folivorous species. Whereas if they did not possess bacteria capable of digesting gum, the folivorous niche would have been unavailable to them. This is an interesting yet controversial idea. Perhaps, not only trees, insects and fruit, but also gum played a role in the early evolution of primates.

2.5 The role of diet in the emergence of primates

Diet is an influential factor in all available hypotheses about the environmental impetus for the evolution of primates. This may be related to the fact that teeth are most-commonly preserved in the mammalian fossil record, and therefore fossil taxa are included in or excluded from Primates based on dental morphology. A syllogism applies: taxonomic distinctions (e.g., nonprimate versus primate) are based on dental morphology; differences in dental morphology in a lineage are perhaps due to differences in diet; therefore, taxonomic distinctions are perhaps based on differences in diet.

Dietary investigations are not just important because they help to draw taxonomic distinctions. Dietary reconstructions can also shed light on ecological relationships between synchronous, sympatric taxa. For example, several paleontologists have suggested that the plesiadapiforms became extinct because they were out-competed by rodents (see Maas *et al.*, 1988). For this to be plausible, these two groups must have been competing for the same resources (e.g., the same food). Thus, a hypothesis of dietary preference is necessary for reconstructing paleoecological relationships. The composition of an animal’s diet drives many of its behaviours. Habitat, locomotion, social organization, mating patterns and anatomy (including body size) are all influenced by and influence diet (e.g., Hladik, 1979).

Thus we can infer diet from many aspects of behaviour and anatomy, and once diet is established, we can better characterize many aspects of primate ecology (e.g., range size and social structure).

Dietary investigations are also important because they generate a fuller understanding of the biology of extinct taxa. Most of the taxa that have ever lived are extinct, therefore understanding the biology of extinct taxa is crucial to making generalizations about the biology of extant taxa and about the processes of life. Not only is the present the key to the past, but the past is the key to the present.

Finally, dietary investigations are important because they paint a more complete picture of the individual extinct taxa. I believe this has intrinsic importance.

2.6 Dietary hypotheses that pertain to early primates

2.6.1 *Extant primates*

The lemurs of Madagascar show a wide variety of dietary preferences from highly folivorous forms (e.g., *Lepilemur*, *Avahi*) to highly insectivorous forms (several mouse lemurs) (Charles-Dominique, 1977). The Malagasy lemurs are represented in my study by *Lemur catta*. This species is primarily folivorous, specializing on immature leaves, stems and buds, but it does consume fruits and flowers in large quantities (Kay *et al.*, 1978; Ganzhorn, 1986; Yamashita, 1996).

The lorises of south-east Asia are poorly studied. The few observations of their feeding behaviour suggest they are mainly animalivorous: they prey on insects and small vertebrates. They also eat fruit in variable quantities. *Loris tardigradus* is highly insectivorous; it consumes “mainly insects, also small lizards and birds” (Napier and Napier, 1967, p. 203; see also Chivers and Hladik, 1980). *Nycticebus coucang* is very poorly studied. The few field observations of the slow loris suggest it consumes a smaller proportion of insects than does the slender loris (*L. tardigradus*), and that it consumes fruit, leaves and seeds as well (Elliot and Elliot, 1967; Napier and Napier, 1967; Hladik, 1979).

The galagos of sub-Saharan Africa are dietary generalists. Most consume fruit, insects, gum and other plant parts in variable quantities, though there is a great deal of dietary interspecific variability (e.g., Cordell, 1991). I tested *Otolemur crassicaudatus*, the thick-tailed galago. Though there is some disagreement as to the relative importance of the constituents of its diet (Cordell, 1991), this species consumes gum in large quantities, insects in small quantities and fruit in smaller quantities (Charles-Dominique and Bearder, 1979; Harcourt, 1980). This species may also feed on nectar (Sussman, 1978).

Tarsius spectrum, representing the extant Tarsiiformes, is perhaps the most insectivorous primate. It consumes almost exclusively insects and small vertebrates (Napier and Napier, 1967; Jablonski and Crompton, 1994; Crompton *et al.*, 1998).

Though *Tupaia glis* is not considered a primate here, it was tested for comparative purposes and because it is currently considered by some to be the closest sister group to euprimates (e.g., Kay *et al.*, 1992). The common tree shrew is primarily insectivorous, though the role of fruit in its diet has been stressed recently (Emmons, 1991).

2.6.2 *Plesiadapiformes*

There is disagreement as to the dietary preference of individual species; however, there is consensus as to the general dietary trends in this group. The earliest plesiadapiforms are small and show insectivorous adaptations of the post-canine dentition. During the Paleocene, several lineages developed molars with low, bulbous cusps and a diastema between the incisors and the premolars. These adaptations suggest a trend toward more herbivorous diets (Szalay and Delson, 1979).

The Plesiadapidae are relatively well-known. Several plesiadapids develop herbivorous adaptations in the dentition. Gingerich (1976) believes that several of the later and larger plesiadapids were ground-dwellers consuming primarily stems or seeds (*Chiromyoides*). By contrast, Covert (1986) suggests that the genus *Plesiadapis* is made up of frugivores. The crenellations on the molars of many *Plesiadapis* species are reminiscent of those on the molars of some bats. These structures have been suggested as adaptations to squeezing juices out of soft fruit (Gingerich, 1976). I tested two plesiadapids: *Plesiadapis churchilli* and *Plesiadapis fodinatus*.

The distinct plagioulacoid⁶ dentition of the carpolestids is a puzzle to functional morphologists. No modern dentition resembles it closely. Perhaps the most comprehensive study on diet in carpolestids was performed by Biknevicius (1986). She concluded that the dentitions of carpolestids are best-suited to processing food items that possess a “soft interior covered by either a brittle or a ductile coat”, such as “invertebrates, nuts, and seeds” (Biknevicius, 1986, p. 157). She suggested that the blade-like p4 was used as a ‘wedge’ to divide resistant foods into smaller pieces, which were then crushed by the cuspidate molars. The action of a wedge works well on ductile foods, but poorly on brittle foods (Strait, 1997), such as seed coats.

⁶ That is, characterized by a laterally compressed, enlarged, bladelike lower premolar that occludes with several upper teeth. Usually there is a diastema present anterior to the enlarged lower premolar. Plagioulacoid is present in carpolestids, saxonellids, some multituberculates and some marsupials.

Others have suggested that carpolestids were adapted to a frugivorous-insectivorous diet (Covert, 1986, for *Elphidotarsius* only), a frugivorous-graminivorous⁷ diet (Kay and Cartmill, 1977), or an insectivorous diet (Rose and Fleagle, 1985a). Some authors have suggested an even more complicated diet for these enigmatic creatures. Rose (1975) suggested they ate hard fruit and hard seeds and perhaps insects too. Clearly the functional morphology of the carpolestid dentition is not fully understood. However, most authors agree that they become increasingly specialized through time, from *Elphidotarsius*, through *Carpodaptes*, to the highly specialized *Carpolestes* (e.g., Rose, 1975; Rose and Fleagle, 1985a). To my knowledge, no dietary hypotheses have been advanced for *Carpocristes* and *Chronolestes* (Beard and Wang, 1995), the new - alleged - carpolestid genera.

I tested two carpolestid species: *Carpodaptes hazelae* and *Carpolestes dubius*. No published dietary hypothesis applies to either of these species individually. With the exception of Covert's (1986) comment on the diet of *Elphidotarsius*, all such inferences refer to the family as a whole.

The remaining plesiadapiform taxa in my study are *Phenacolemur praecox* and *Plesiolestes problematicus*.

A great deal of attention has been paid to the peculiar molar morphology of *Phenacolemur*. It possesses distinctively large talonid basins that appear effective for processing soft, juicy fruit (Rose and Fleagle, 1985a; Covert, 1986), gum or nectar (Kay and Cartmill, 1977). Williams (1980) suggested it was adapted to a fruit and insect diet. Conversely, the loss of the anterior premolars and the large, wide p4 suggest a seed-cracking function for this dentition (Szalay, 1972b). Thus, *Phenacolemur* may have been eating the softest foods available to primates, and/or the hardest!

Plesiolestes problematicus, as befits its specific epithet, is enigmatic with respect to diet. It possesses a rather primitive, generalized (relative to other plesiadapiforms) dentition, with subtle herbivorous adaptations (Szalay and Delson, 1979). Gunnell (1989, p.22) considers this genus to be omnivorous, whereas Covert (1986) calls it insectivorous, and Szalay and Delson (1979) call it frugivorous.

There is a great deal of disagreement as to the dietary preferences of individual plesiadapiform genera. Additionally, categories like 'insectivorous' and 'frugivorous' are so vague that most plesiadapiforms may easily fall into the wide zones of overlap between them. Currently, primatologists are attempting to refine dietary categories with reference to the physical properties of food (e.g., Yamashita, 1996; Strait, 1997). A more refined dietary vocabulary will reduce the confusion produced by many paleodietary studies.

⁷ 'Graminivorous' describes an animal that eats nuts and/or seeds.

2.6.3 Euprimates

There is much less confusion concerning the hypothetical diets of the Eocene euprimates. Perhaps this is because they have reasonably good modern analogues among the extant prosimians.

Most notharctine adapids are herbivores, their dietary niches correspond roughly to those occupied by extant lemurs. *Cantius* is considered by both Covert (1986) and Fleagle (1999) to be a frugivore. It possesses bulbous molar cusps and wide shallow basins. Its molars resemble those of some species of *Plesiadapis*. Most consider *Notharctus* to be a folivore (e.g., Rose and Fleagle, 1985b; Covert, 1986; Conroy, 1990; Fleagle, 1999), or at least an herbivore (Cartmill, 1972; Szalay and Delson, 1979). *Smilodectes* is considered by most to be a more folivorous version of *Notharctus* (Szalay and Delson, 1979; Covert, 1986; Fleagle, 1999) because of the high degree of shear in the molars of the former. Covert goes out on a limb to say “*Smilodectes gracilis* also was most certainly folivorous” (Covert, 1986, p. 351).

I tested specimens of *Cantius eppsi*, *Notharctus sp.* (see footnote 2, above, that explains why I have not provided a specific epithet), and *Smilodectes gracilis*. Considering the consensus in the literature with respect to the diets of these notharctines, it would be contentious if my results suggested dietary preferences other than those hypothesized.

Little has been inferred about the diets of the omomyids tested. Most agree, however, that most omomyids were insectivores (Covert, 1986), largely because most of them were very small. I tested two omomyids: *Tetonius matthewi* and *Arapahovius gazini*. Covert suggests that *T. matthewi* was an insectivore that may have consumed fruits also. Szalay and Delson (1979) suggest that it was an omnivore that concentrated on fruits. The only reference to the diet of *A. gazini* (Covert, 1986) suggests it consisted of insects mainly.

2.6.4 Regretted omissions

Several plesiadapiform families are dentally unique. The Picodontidae, for example, possess a highly derived dental morphology reminiscent of bats in some respects (Szalay, 1968b). However, picodontids are undoubtedly plesiadapiforms (Williams, 1980). The deep, wide and wrinkled molars in this family resemble those of certain plesiadapids. They are thought to have specialized on a “pulpy fruit and/or nectar and flowers diet”

Williams, 1980, p.212). A study of the functional morphology of the picrodontid dentition would likely prove very fruitful.

The saxonellids are also intriguing. Their post-canine morphology parallels that of carpolestids in some ways (e.g., plagiulaacoid lower premolars), but it is radically different in others (upper premolar morphology). Saxonellid dental morphology is unique among mammals (Fox, 1991) and functional hypotheses are difficult to construct as there is no good modern analogue for these extinct primates.

Unfortunately, no appropriate specimens of picrodontids or saxonellids are known to me. Hopefully, future field work will yield more nearly complete picrodontid and saxonellid specimens. Appropriate specimens of the micromomyid species *Micromomys fremredi* and *Tinimomys graybulliensis* were available. However, these specimens were either too fragile to cast, or when cast, they proved too fragile to test. Perhaps future developments in casting technology will make possible the mechanical testing of such small and fragile specimens.

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Chapter 3: Paleoecology of the Holarctic Paleocene and Eocene

3.1 The importance of paleoecology

Evolution is a dynamic process that operates in a complex system. To understand the biology of an extinct organism, it is necessary to understand the other components of its system, namely, its environment. As this study focuses on the evolution of the earliest primates, the environment of concern is that of the Paleocene and Eocene of North America, Europe and Asia.

It is likely that numerous environmental factors affected the evolution of the earliest primates. These include the organisms upon which they preyed, their predators, their competitors and various climatic, vegetational and landscape influences. This chapter attempts to place the origin and early evolution of primates in context. I focus on the prey of primates because this thesis focuses on diet. This chapter will also touch on climatic and vegetational features of the Paleocene and Eocene as these affect the kinds of food that might have been available to the first primates and their nonprimate ancestors.

3.2 The distribution of the earliest primates

Plesiadapiformes are known from the latest Cretaceous to the late Eocene (Lancian to Uintan North American Land Mammal Ages) in North America and a slightly more restricted range in Europe (Szalay and Delson, 1979; Fleagle, 1999). The fossil record of plesiadapiforms is primarily Paleocene; the only Cretaceous record is that of a single tooth (Van Valen and Sloan, 1965). Few plesiadapiforms are found in sediments younger than the early Eocene, though *Ignacius* and *Phenacolemur* are late-surviving exceptions. Despite the poor Cretaceous record of primates, it is likely that the plesiadapiform species branched off from a nonprimate lineage during that period. Therefore, some attention will be paid to environmental conditions in the Late Cretaceous.

The plesiadapiforms in this study are primarily Paleocene and all are from North America. *Plesiadapis* is known from the late Paleocene to the early Eocene of North America and Europe (Fleagle, 1999). *P. churchilli* characterizes the Tiffanian Zone 4 (late Paleocene) and *P. fodinatus* characterizes Tiffanian Zone 5 (also late Paleocene) (Gingerich, 1976). *Carpodaptes* is known from the Tiffanian, and perhaps also the latest Torrejonian of western North America. *Carpodaptes hazelae* is known from the same. *Carpolestes* is known from the latest Tiffanian to the Wasatchian (early Eocene) and *Carpolestes dubius* is

known from primarily the Tiffanian-Clarkforkian (early Eocene¹) boundary.

Phenacolemur is known from the Tiffanian to the early Bridgerian of North America and the Sparnacian (early Eocene) of the Paris Basin. *Phenacolemur praecox* is early Wasatchian (Bown and Rose, 1976). *Plesiolestes* is primarily Torrejonian, as is *Plesiolestes problematicus* (Jepsen, 1930; Bown and Gingerich, 1973).

Adapids are known from the early Eocene (Wasatchian) to the late Eocene (Uintan) of North America, from the early Eocene (Neustrian) to the early Oligocene (Headonian) in Europe, with a possible Eocene to Miocene record in Asia (Szalay and Delson, 1979). However, most of the evolution of the Adapidae took place during the Eocene.

The adapids studied here are from the early and middle Eocene of North America and Europe. There is considerable disagreement as to what species should be included in *Notharctus* (see Chapter 2). Regardless, this genus is confined to the Eocene of North America, from the Wasatchian to the Bridgerian. The *Notharctus* specimens I used in this study are from the Wasatchian (early Eocene) and Bridgerian (middle Eocene) (Szalay and Delson, 1979; Fleagle, 1999). They are likely either *N. venticolusi* or *N. tenebrosus*. The taxonomic composition of *Cantius* is at least as nebulous. It has both a North American and a European distribution. *Cantius eppsi*, the species tested here, is from the Sparnacian (early Eocene) of England (Simons, 1962). *Smilodectes* is known from the Bridgerian of North America; *Smilodectes gracilis* is known from the same (Szalay and Delson, 1979).

The Omomyidae are known from the early Eocene (Wasatchian) to the early Miocene (Arikareean) in North America and from the early Eocene (Neustrian) to the early Oligocene (Suevian) in Europe (Szalay and Delson, 1979). *Altanius*, a possible omomyid, is known from the early Eocene of Mongolia (Dashzeveg and McKenna, 1977), though this primate might be a plesiadapiform (Rose and Krause, 1984). Another possible omomyid, *Altiatlasius*, is known from the late Paleocene of Morocco (Sigé *et al.*, 1990). Most omomyid species are confined to the Eocene, with some species persisting to the early Oligocene. One noteworthy exception is the unusual genus *Ekgmowechashala* from the early Miocene of South Dakota and Oregon. But for a few exceptions, the Eocene is the stage for the evolution of the earliest euprimates: the adapids and the omomyids.

¹ There is some controversy over whether Clarkforkian faunas should be considered Paleocene or Eocene. Gingerich (1976) and Rose (1975, 1981) provide good summaries of the issue. Since the 1920's, the Clarkforkian has usually been considered Paleocene (Rose, 1981), but Gingerich suggests it is Eocene based on similarities to the Paris Basin fauna (Gingerich, 1976). Rose (1981) urges that the end of the Paleocene is marked by the end of the *Plesiadapis gingerichi* zone in North America because this corresponds most closely to the end of the *Plesiadapis tricuspidens* zone (the latest of the Paleocene zones in Europe) in the Paris Basin. Here, I have chosen to refer to the Clarkforkian as part of the Eocene, primarily for simplicity and ease of communication, despite the compelling arguments of Rose (1981). See also Aubry (2000).

The omomyids tested here are from the early Eocene of North America. *Tetonius* is from the early Wasatchian of western North America, as is *T. matthewi*, the species used in this study (Bown and Rose, 1987). *Arapahovius* is from the Wasatchian of western North America, as is *A. gazini*, the species used in this study (Rose, 1995).

Primates suffered from extinctions at the beginning of the Eocene and again at the beginning of the Oligocene in North America and Europe. By the middle Oligocene, very few primate species were left at high latitudes. Therefore, primate evolution on the Holarctic continents took place primarily during the Paleocene and Eocene. Some species of nonhuman primates exist today in tropical or subtropical areas of southern Europe and Asia, but since Oligocene times, most have been confined to relatively low latitudes.

3.3 Paleocene and Eocene climates in North America and Europe

In the Paleocene and Eocene, the continents were positioned much as they are today, though the Atlantic was narrower and India was still an island until the early Eocene (Adams, 1981; Beck *et al.*, 1998; Beard and Dawson, 1999). North America and Europe were connected by a land bridge, as were North America and Asia. However, Europe was separated from Asia by the Turgai Straits throughout much of the early Tertiary (e.g., Wicander and Monroe, 1993). Despite basic geographic similarity, climatic conditions in the Paleocene and in the Eocene were very different from those we experience today.

The Cretaceous was one of the warmest periods in Earth's history, but near the end of the Age of Reptiles mean annual temperatures began to drop (Tiffney, 1981). Shortly after the Cretaceous-Tertiary (K-T) boundary event, global temperatures were low and primary successional ferns briefly dominated floras around the world (Wing and Tiffney, 1987). Gymnosperms and angiosperms recolonized North America and Europe rapidly, but early Paleocene floras were depauperate relative to those of the Cretaceous. During the Cretaceous, angiosperms were small, weedy, opportunistic and transient, populating marginal environments; gymnosperms dominated swamps and forests (Tiffney, 1984). After the K-T event, taxodiaceous conifers continued to dominate the swamps, but angiosperms thrived on silty, nutrient-poor substrates (Wing and Tiffney, 1987).

The early Paleocene Holarctic was characterized by moderately warm temperatures, high precipitation and some seasonality (Crane *et al.*, 1990). This seasonality may have favoured the spread of the deciduous angiosperms at the expense of the formerly dominant broad leafed evergreens (Stewart and Rothwell, 1993). Angiosperm floras lacked diversity throughout the Paleocene, though many modern families were represented (Tiffney, 1981; Manchester, 1999). North American and European Paleocene floras were probably much

like the mixed mesophytic, temperate forests of southeast Asia and the Atlantic coastal plain of North America today (Crane *et al.*, 1990).

A warming trend began in the late Paleocene (primarily Tiffanian); temperatures reached a maximum in the Wasatchian. Mean annual temperatures escalated from 12°C in the Tiffanian, to 19°C in the Clarkforkian, to 21°C in the Wasatchian (Bao *et al.*, 1999; Wilf, 2000). During this time, subtropical plants invaded the North American and European floras (Hickey, 1977; Tiffney, 1981). Subtropical species gradually replaced temperate ones; the low diversity of floras that characterized the early Paleocene persisted into the early Eocene (Tiffney, 1981). The mosaic of temperate and subtropical plants in an equable, warm environment is unique: it is unknown in modern floras.

Large herbivores disturb vegetation as they forage, therefore plants do well to grow far apart in their presence. Wing and Tiffney (1987) suggested that the absence of large herbivores following the Cretaceous-Tertiary event allowed closed forests to develop during the Paleocene. The closed forest of the Paleocene included angiosperms and promoted the evolution of several angiosperm innovations. Small seeds are optimal in well-lit conditions because they develop rapidly; however, under low light, large seeds or fruits are optimal because they provide more nutrition to the developing embryo (Tiffney, 1984; Wing and Tiffney, 1987). Seeds became progressively larger as forests became more closed and competition grew fiercer. Yet, large seeds are not easily dispersed by the wind; they require biotic agents for dispersal. Thus is the stage set for the appearance of small-bodied frugivores and graminivores.

A diaspore is a “reproductive unit [of a plant] that is dispersed or sown” (Tiffney, 1984, p. 551). A diverse array of large and small diaspores are known from the Paleocene. However, the first very large and fleshy fruits appear only in the latest Paleocene and earliest Eocene (Tiffney, 1984). The first euprimates appear at the same time (see section 3.2, above). The Paleocene fossil record reveals a vast array of small herbivores. Many of these were arboreal and many were probably consuming and dispersing angiosperm diaspores. Wing and Tiffney (1987) suggest that the evolution of large angiosperm diaspores and the evolution of small-bodied mammalian frugivores influenced one another considerably. Positive feedback in these two groups may have led to the progressive specialization of fruit and frugivores to one another. This hypothesis resembles the angiosperm co-evolution hypothesis that Sussman (1991) used to explain the origin of the Primates.

A brief (~150 000 years) warming event took place around 55 million years ago, at the Tiffanian-Clarkforkian boundary. A substantial decrease in the carbon 13 isotope ($\delta^{13}\text{C}$) in benthic foraminifera attests to a sudden climatic change at this boundary (Dickens *et al.*, 1997; Bao *et al.*, 1999). This climatic change has been attributed to a significant

release of methane hydrate (CH_4 trapped in a water lattice) into the atmosphere from under oceanic crust (Dickens *et al.*, 1997). This would have released an abundance of the carbon 12 isotope into the air and water, thus decreasing the proportion of other carbon isotopes taken up by foraminifera. A brief cooling event, lasting about 600 000 years, followed (Bao *et al.*, 1999). Afterward, temperatures rose again until the Wasatchian. This event may have exacerbated late Paleocene extinctions (e.g., that of most plesiadapiforms) and promoted subsequent early Eocene radiations (e.g., that of euprimates).

Throughout the Eocene, modern angiosperm families continued to appear, such that most were present by the end of the epoch (Stewart and Rothwell, 1993). Precipitation and temperature increased through the Eocene until the Wasatchian, and remained high until the late Eocene. Forests were dominated by subtropical species. Eocene floras of the arctic resemble those of the modern-day Atlantic coastal plain in North America. Eocene floras known from the Pacific Northwest of North America resemble those of modern-day Central America (Tidwell, 1975).

A major decline in precipitation occurred in the late Eocene, followed by a decline in temperature. Warm temperate conditions returned to most of North America and Europe. Precipitation and temperature continued to drop throughout the Oligocene (Stewart and Rothwell, 1993) while seasonality increased (Tiffney, 1981). Increased seasonality likely favoured the emergence and spread of grasses, as these plants cope well with variable seasons. Forests became more open as a result of the success of grasses and herbs; diaspore size decreased in the well-lit environments (Tiffney, 1981). This trend may have contributed to the decline of the early Holarctic primates (especially Adapidae and Omomyidae) and their eventual extinction.

3.4 Food for the earliest primates

3.4.1 Food derived from plants

Much of the food consumed by herbivorous primates today comes from angiosperms. It consists of fruit, nuts, seeds, leaves, buds, gum, bark and sometimes tubers (Napier and Napier, 1967). Many of these food sources were available in the forests of the Paleocene and Eocene of North America and Europe. Large, fleshy fruits and nuts are known only as far back as the early Eocene (Tiffney, 1984), though this does not mean that they were *not* present in the Paleocene. Certainly there were large, moderately fleshy fruits and nuts in the Paleocene (Tiffney, 1984). Many of the fossil angiosperms of the

Paleocene and Eocene have been assigned to families that persist today (Hickey, 1977; Manchester, 1999). Even some Recent genera have representatives in the Paleocene and/or Eocene fossil record (Manchester, 1999).

To make my simulation experiment as realistic as possible, I selected foods derived from plant families that have Eocene and/or Paleocene representatives. Clearly phylogenetic proximity does not necessarily equate to similarity in the material properties of food. However, it is probably the best estimate available because material properties are but grossly estimated from plant fossils (Tiffney, 1984; Stewart and Rothwell, 1993). Moreover, the extant plant foods I used are probably very different from their extinct relatives, even if they are assigned to the same genus. Once again, it is necessary to make approximations. These approximations are partly justified by the presence of several modern angiosperm families in the Paleocene and Eocene.

The family Anacardiaceae (sumachs and pistachios) is well-known from fruits preserved in the Eocene of Oregon and England (Manchester, 1999). These were relatively modern. Leaves of *Rhus* (sumach) are known from the Cretaceous, Eocene and Oligocene (Tidwell, 1975; Manchester, 1999). The use of sumach fruits in my study is particularly justified as these were present in the environment of the earliest primates. *Pistacia* nuts are probably more ‘fleshy’ than their early Tertiary confamilials; however, they have material properties that were almost certainly represented in the early Eocene at the latest (Tiffney, 1984).

Berberidaceae are known from fossil *Mahonia* (Oregon grape) in the Eocene (Tidwell, 1975; Manchester, 1999). The barberry, *Berberis*, is assigned to the same family. This berry is ovoid (0.5-1cm long), fleshy and juicy with long (2-3mm), soft seeds. It is readily available as a cultivated shrub in Edmonton. Therefore, I chose to use it in this study as a representative of its family and small fleshy fruit in general.

The elder family, Caprifoliaceae, is known from fruit in the Eocene of the United States and England. The genus *Diplopelta* is the most common representative (Manchester, 1999). The elder, *Sambucus*, belongs to this family. The fruit of the elder, the elderberry, is a small (diameter=~0.5cm) spherical, pulpy berry with a rather thin skin and plenty of juice. Seeds are small (1-2mm long) and very hard. This genus also grows in Edmonton and is used in this study as a representative for its family and small fleshy fruit in general.

Fagaceae, and particularly *Quercus*, the oak, is known from wood and leaves in the Cretaceous (Tidwell, 1975) and nuts/acorns and leaves from the Eocene of Oregon (Manchester, 1999). The use of oak leaves in this study is justified because they and leaves with similar material properties were available to early primates.

Aceraceae, and particularly *Acer*, the maple, is known from samaras in the late Paleocene and from leaves in the North American Eocene (Manchester, 1999). The earliest record of this genus is Cretaceous (Tidwell, 1975). Just as for the oak, the experimental use of maple ‘seeds’ or samaras is justified. Though this part of the maple must harbour little nutritional value, it was present in the Paleocene and Eocene forests of North America.

Though the rose family is very diverse today, it is rare or absent in the Paleocene. The Rosaceae is represented in the middle Eocene fossil record of British Columbia and Washington State (Manchester, 1999). These representatives have been assigned to the genus *Prunus*, that contains plums, peaches, cherries and many other fleshy-fruit-bearing trees. The Eocene record of *Prunus* justifies the use of the common plum in my experiment. Also I have used plums to represent large fleshy fruit. The rose itself, *Rosa*, is only known as far back as the early Oligocene (Oregon)(Manchester, 1999). However, it is likely that flowers possessing similar material properties existed at least as far back as the earliest Paleocene (Raven *et al.*, 1992).

Acacia, whence gum arabic is derived, is assigned to the family Leguminosae. Several genera of the very diverse Leguminosae are known from the Eocene Green River flora (Tidwell, 1975). Though I know of no fossilized gum or exudate from this family, it is quite possible that gum-exuding angiosperms existed in the early Tertiary. Hypotheses, such as that suggested by Nash (1989), depend upon the presence of gum-exuding plants in the early Tertiary.

Many modern gymnosperm families were present in the Paleocene (Tidwell, 1975). Extinct members of the family Cupressaceae, which includes *Juniperis*, are known from cones in the Paleocene of Alberta, Saskatchewan and Wyoming (McIver and Basinger, 1990; McIver, 1992; Manchester, 1999). I tested the cones of *Juniperis*. These resemble berries and possess physical properties similar to dry, pulpy fruits. The genus *Juniperis* is known from the Oligocene of Montana and perhaps from the Cretaceous of Alberta (Tidwell, 1975).

The record of the Ginkgoaceae is extensive. Ginkgos are known as far back as the Jurassic (Manchester, 1999). Additionally, ginkgo leaves are also known from late Paleocene floras (Crane *et al.*, 1990). These leaves are nearly indistinguishable from leaves of extant *Ginkgo* (Crane *et al.*, 1990).

3.4.2 Food derived from animals

Most of the invertebrates and small vertebrates eaten by extant prosimians today were present in the Paleocene and Eocene. Chickens (*Gallus*) are not known from the

Paleocene or Eocene (Feduccia, 1996). However, the part of the animal I have tested, namely skeletal muscle, has probably had roughly the same material properties in birds since birds began to fly. Flight-capable neornithes existed prior to the Paleocene; therefore, the pectoral muscles of flying birds were likely available to early Tertiary primates (Feduccia, 1996). Galliform birds are known from the early Eocene of Wyoming and the late Eocene of France (Feduccia, 1996). The earliest phasianids (i.e., the family that includes chickens) are known from the late Oligocene of Europe (Carroll, 1988).

With the exception of anthophilic (flower-visiting) families, insects have remained conservative since the Mesozoic (Grimaldi, 1999). Members of the Gryllidae, the cricket family, are present in the mid-Cretaceous in South Africa (McKay and Rayner, 1986), though the family itself goes back as far as the Late Triassic (Carpenter, 1953a). Assuming that the material properties of the cricket body have remained the same (or similar) since the Paleocene, my experimental use of the domestic cricket, *Acheta domestica*, is justified.

The Coleoptera are known as far back as the Late Carboniferous, and the family Tenebrionidae (the meal worm family) goes back to the Triassic (Carpenter, 1953b). In fact, larval coleopterans that greatly resemble the extant commercial meal worm are known from a forested, swampy environment in the Paleocene of Alberta (late Torrejonian to late Tiffanian Paskapoo Formation) (Mitchell and Wighton, 1979). Larval coleopterans may have been a substantial food resource for the earliest primates.

3.4.3 Specific food tested

Table 3-1 is a list of the foods I tested. Species identifications of some plants are tentative because 1. the specific taxonomy is contentious (e.g., *Rhus*) or 2. the provenance of specimens is unknown (e.g., *Rosa*). The method for preparing foods for testing is detailed in Chapter 7.

Plate 1 shows several representatives of the specific test foods before and after they were masticated (ten cycles) by *Nycticebus coucang*.

3.5 Summary

If we include plesiadapiforms in the order Primates, then primates probably emerged in the Late Cretaceous and experienced their first major adaptive radiations in the Paleocene and Eocene of Europe and North America. A well-forested land bridge connected North America to Europe until the Oligocene, and a similar land bridge connected North America to Asia (McKenna, 1983). Thus, the Holarctic during the Paleocene and Eocene can be

thought of as a single, gradational environment. Intercontinental dispersal was only possible, however, at high latitudes (Beard and Dawson, 1999). The earliest primates are known from Europe, North America and Asia, and perhaps North Africa. Therefore, the earliest primates were essentially Holarctic species that enjoyed a great diversity mainly in the Paleocene and Eocene. Thus, the environmental conditions that prevailed in the Holarctic Paleocene and Eocene drove the evolution and radiation of the first primates.

The first plesiadapiforms probably lived in a closed, warm-temperate forest or swamp, dominated by broad-leaved conifers. These forests were gradually invaded by deciduous angiosperms as the Paleocene climate became increasingly seasonal. Probably in response to low light levels, angiosperms developed large diaspores. These diaspores would have been attractive sources of food for early primates. If plesiadapiforms were eating these diaspores, there should be evidence of frugivorous or graminivorous adaptations in their dentition.

Small mammals, perhaps plesiadapiforms, acted as dispersal agents for the angiosperms. This relationship grew stronger throughout the Paleocene, and by the end of the epoch, angiosperms were producing very large, fleshy diaspores that resembled today's fruit. At the same time, angiosperms were becoming a more noticeable constituent of the flora and subtropical species were beginning to invade forests at high latitudes as temperatures and precipitation levels rose.

At the end of the Paleocene, temperatures and precipitation levels were high. The warm temperate forest had been replaced by mainly subtropical forests. The Holarctic climate was more equable at the Paleocene/Eocene transition. Most of the plesiadapiforms went extinct at this point, for reasons unknown (see Maas *et al.*, 1988). Perhaps biotic factors were responsible (e.g., competition with rodents) or perhaps it was related to a climatic event, such as the release of oceanic methane hydrate (Dickens *et al.*, 1997). Simultaneously, the first 'true primates' show up in the fossil record of North America and Europe.

The first euprimates diversified into a closed, subtropical forest composed of angiosperms and some conifers. Large, fleshy, modern-looking diaspores were common in

Family	Species	Common name	Food	Description
Aceraceae	<i>Acer negundo</i>	Manitoba maple	samara	seed-like, winged
Anacardiaceae	<i>Pistacia vera</i>	commercial pistachio	endosperm	nut
Anacardiaceae	<i>Rhus typhina</i>	staghorn sumach	fruit	dry, seed-like
Berberidaceae	<i>Berberis thunbergii</i>	Japanese barberry	fruit	small berry
Caprifoliaceae	<i>Sambucus racemosa</i>	Pacific red elderberry	fruit	small berry
Cupressaceae	<i>Juniperis horizontalis</i>	creeping juniper	cone	berry-like, fibrous
Fagaceae	<i>Quercus alba</i>	white oak	leaf	thick, firm
Phasianidae	<i>Gallus domesticus</i>	commercial chicken	breast meat	raw
Ginkgoaceae	<i>Ginkgo biloba</i>	ginkgo	leaf	thin, pliant
Gryllidae	<i>Acheta domestica</i>	commercial cricket	whole body	fresh adult insect
Leguminosae	<i>Acacia senegal</i> (mostly)	gum arabic	exudate	rehydrated powder
Rosaceae	<i>Prunus domestica</i>	common plum	fruit	large drupe
Rosaceae	<i>Rosa x</i> (flower shop, cut)	cultivated red rose	petal	thin, pliant
Tenebrionidae	<i>Tenebrio molitor</i>	commercial meal worm	whole body	fresh larval insect

Table 3-1 Foods tested. Specific foods are grouped in Chapter 8 (results chapter) into general categories based on their material properties rather than on strict anatomical homology. Plants were identified with the help of mainly Steven Williams of the University of Alberta Phytotron. Insects were obtained from a pet store. Chicken, plums and pistachios came from a grocery store and roses came from a flower shop. Gum arabic was obtained from a biological supply company. Other plant materials were obtained from cultivated or wild plants on or near the University of Alberta campus.

the Eocene and the primates may have profited from them. If so, it should be apparent from their dental morphology.

By the late Eocene, the climate was cooler and drier. Grasses began to encroach on the Holarctic forests. Light-adapted, prolific grasses began to push larger trees aside, such that Holarctic forests were much more open in the late Eocene than in the Paleocene and early Eocene. The opening of the forests made way for large-bodied herbivores. At about this time, euprimates began to disappear from North American and European faunas.

Throughout the Paleocene and Eocene, primates had many food resources at their disposal. Many of the modern angiosperm families populated the Holarctic forests as early as the Late Cretaceous. Many more are known from the Paleocene, and by Eocene times, most modern angiosperm families were present. There is no evidence of gum in the fossil

record, but wood-boring insects - that stimulate the production of gum - were present (Carpenter, 1953a, b). Also, leaves, flowers, nuts, seeds and small fruits were present in the Paleocene. Large, fleshy fruits were present by the Eocene. Small vertebrates and invertebrates were abundant in the Paleocene forests (Tiffney, 1984; Carroll, 1988). Birds, which make up an important part of the diet of many extant prosimians (Napier and Napier, 1967), were present in the Paleocene (Feduccia, 1996), as were most of the modern insect families (Carpenter, 1953a, b). Crickets and beetles are known from the Paleocene, and larval beetles resembling *Tenebrio molitor* larvae are known from the Paleocene of Alberta (Mitchell and Wighton, 1979). An extensive menu, much like that tested here, was available to the earliest primates in the early Tertiary Holarctic.

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Chapter 4: Morphometric¹ methods for inferring diet in fossil primates

4.1 Basic principles

4.1.1 *The basis of functional morphology*

Students of functional morphology must be prepared to assume that there is a causal interrelationship between the physical dimensions of a biological structure and the way it is used by the organism. This causal interrelationship can be explained with an example: those individual gibbons that possess arms that bear tensile loads poorly are more likely to fall from the branches of a tree and either die or injure themselves. Gibbons that can better hang from branches will secure food more successfully and gain access to more mating opportunities. As a result, the genes that code for tensile-load-bearing arms will eventually begin to appear with a greater frequency in the gibbon population. In this manner, evolutionary theory predicts that, over time, the relationship between the morphology and the function of a biological structure will strengthen, so long as functional demands remain constant. The assumption that form and function share a strong relationship hinges on another assumption, that of optimization.

The notion of ‘optimization’ refers to the condition whereby organisms waste as little as possible of the matter they acquire and as little as possible of the energy they produce. Organisms become optimized over evolutionary time because, assuming that all individuals of a species have an equal chance to access resources, the individual that wastes its metabolic resources is less likely to produce useful structures such as a lustrous coat of fur, strong bones, sharp claws, etc. This wasteful individual will be competitively excluded by more ‘optimal’ individuals. In some cases, the optimization model falls apart because some individuals have greater access to resources, and can therefore, afford to waste them without compromising their relative fitness. The model also fails when resources are abundant and competition is minimal.

4.1.2 *Dental-dietary adaptations*

The primary function of the premolar and molar teeth in most primates is to break ingested food items into small fragments. This action is called *chewing* or *mastication* and it helps to optimize feeding by increasing the surface area to volume ratio of food, such that

¹ That is, measuring form.

more surface is exposed to the digestive juices for chemical breakdown (Chivers, 1982; Lambert, 1998).

In studies of diet in fossil primates (and other fossil mammals as well), both assumptions, that of the tight relationship between form and function and that of optimization, are taken for granted. The form of the teeth is strongly related to their function. This is an old observation: Aristotle noted it in the third century B.C.:

“Now human teeth are admirably adapted for the purpose that all teeth subserve: the front ones are sharp, to bite up the food; the molars are broad and flat, to grind it small” (translated by Peck, 1937, p. 209).

Furthermore, the form of the premolar and molar teeth is strongly correlated to diet (Kay, 1975; Kay *et al.*, 1978; Seligsohn, 1977; Yamashita, 1996; 1998). A brief history of the work on the dental-dietary relationship is given by Kay (1975).

Some functional morphologists fail to consider the material properties of teeth and foods when inferring diet in an extinct organism; it suffices to draw parallels between the tooth morphology of extant primates (with empirically knowable diets) and those of their extinct relatives (Gingerich, 1976; Kay and Cartmill, 1977; Szalay and Delson, 1979; Covert, 1986). This approach works well when the mammal under study is a dietary specialist, such as a cat or a cow, and when the dietary inferences made are very general. If you find a fossil mammal that has a very feline dentition, chances are it was not a specialized grazer.

More recently, several authors (Lucas and Luke, 1984; Strait, 1993; Yamashita, 1996; Strait, 1997; Crompton *et al.*, 1998; Strait and Vincent, 1998; Yamashita, 1998) have taken a more rigorous approach to the relationship between diet and dental morphology. They suggest that it is necessary to understand the physical principles underlying food breakdown to make inferences about diet from tooth morphology alone. These authors often draw parallels between tooth features and man-made tools.

4.1.3 *The concept of diet*

One complication is the question: what constitutes a diet? Most primates eat more than one kind of food. Diet can be viewed as the sum of all the kinds of food that an animal consumes, preferably with some reference to the relative proportions of the various kinds of food, and the seasonal and intraspecific variation in diet.

Conversely, the diet of a primate could be defined by the food it consumes more than any other food. Some primates, such as many South American marmosets (e.g., *Callithrix flaviceps*), consume more soft tree exudate than anything else (Ferrari, 1998). Many bats and one species of lemur, *Lemur mongoz mongoz*, (Sussman, 1978) consume more nectar than anything else. It is hard to imagine how a substance like soft tree sap or nectar can influence the shapes of teeth over time - these substances need not even contact the teeth to be consumed effectively. In fact, it is more adaptive for a primate with such a diet to have flat teeth or no teeth at all because sap and nectar are likely to get caught in the relief of a molar and fail to be digested. However, marmosets, fruit bats and many other soft-food consumers possess highly complex molars. Perhaps this is because marmosets and fruit bats do not consume *only* soft foods²; insects are included in the diets of most consumers of soft foods (e.g., Ferrari, 1998). It is very likely that the physical properties of these insects are responsible for the complex shapes of the molars in these mammals.

Perhaps then, it is not the kind of food *most* consumed that is correlated to tooth morphology, but rather the most *physically demanding* kind of food that is regularly consumed.

There are many pitfalls to inferring diet in extinct primates when tooth morphology is used alone. It is necessary to consider assumptions about the relationship between form and function and about optimization. Furthermore, one must be clear as to how diet is being defined before one accepts dietary inferences in extinct *or* extant animals.

Several dimensions on the post-canine teeth of primates may be informative with respect to dietary preference. I have selected three morphometric methods from the literature. Each of these methods uses several dental dimensions to infer diet. Apart from simple comparisons to living taxa, these three methods appear to be the most commonly used for inferring diet from post-canine tooth morphology. Although they all focus on extant taxa, they are of use to paleontologists because diet cannot be *observed* in extinct taxa, rather it must be *inferred*.

In an effort to compare the usefulness and predictive power of the following three morphometric methods, I have applied each method to the dentitions tested in the mastication machine. In Chapter 8, the results of the chewing experiment are compared with the results of the morphometric studies.

² It is also possible that these teeth are used for behaviours other than mastication (e.g., grooming, prehension). However, it is difficult to envision such behaviours for molars.

4.2 Seligsohn's method

4.2.1 *Seligsohn, 1977*

Seligsohn (1977) performed a detailed analysis on the molars of several species of strepsirrhine (i.e., prosimians minus tarsiers) primates. He was searching for a correlation between the known diets of these primates and topographical features of their molars. The aim was to discover easily measurable features of the molars that could be used to make confident inferences about diet in fossil primates. He also examined whether or not these features were correlated to taxonomy or molar size.

Using a stereoscope with an attached camera lucida, Seligsohn drew the upper and lower second molars of 27 species of strepsirrhines in both occlusal and labial views. Several measurements (thought to be functionally significant) were taken on the resulting scale drawings (pp. 21-31 of Seligsohn, 1977). Thirty-seven indices were calculated by combining these measurements (pp. 33-34 of Seligsohn, 1977). The indices for all primates studied were then plotted in histograms. The species (the columns of the histograms) were arranged from left to right in five dietary categories: insects and small vertebrates preferred, fruits and gums secondarily preferred (the greater proportion of insects and small vertebrates in the diet, the further left a species plots on the histogram); fruit and gums preferred, insects and small vertebrates secondarily preferred; fruits and gums preferred, leaves secondarily preferred; leaves preferred, fruits and gums secondarily preferred; and stems preferred, leaves secondarily preferred.

Seligsohn observed that several of the indices he used varied with dietary preference in the manner predicted (p. 105). From these, I chose four indices that Seligsohn suggested are particularly informative with respect to diet:

- VI: height of paracone / width of paracone
- VII: height of paracone / square root of: M2 length x M2 width
- VIII: height of paracone / width of labial portion of M2
- XXXV: angle between the cristid obliqua and the postcristid

Seligsohn predicted (p. 36) that species would rank according to dietary preference in the following order (descending) for indices VI, VII and VIII: insects, leaves (species with cross-lophed molars), stems, leaves (species without cross-lophed molars) and fruits. Thus, species that eat mostly insects should score high for these indices and those specializing in fruit should score low. For index XXXV, he predicted the following order: leaves (without cross-lophs), fruits, stems, leaves (with cross-lophs) and insects. These

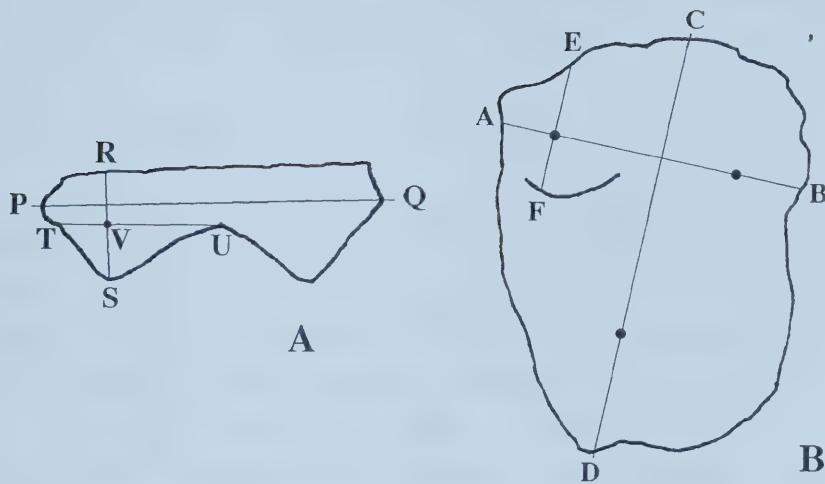


Figure 4-1 Sketches for Seligsohn's indices VI-VIII. Both are drawings of the left M2 of the test specimen of *Notharctus sp.*. A, labial view (dorsal is up, anterior is to the left). P is the most mesial point on the tooth crown in labial view; Q is the most distal point. R-S is perpendicular to P-Q and connects the apex of the paracone (S) to the cemento-enamel junction (R). T is the most dorsal point on the preparacrista; U is the most dorsal point on the centrocrista. T-U is the width of the paracone. V-S is the height of the paracone. B, occlusal view (anterior is to the left, labial is up). A-B is a line through the apex of the paracone and the apex of the metacone and is the length of the M2. C-D is perpendicular to A-B, is drawn through the apex of the protocone and is the width of the M2. E-F is parallel to C-D, is drawn through the lingual limit of the paracone and the apex of the paracone; E-F is the width of the labial portion of the M2.

rankings are largely borne out by Seligsohn's results for the above indices.

I also chose to examine three additional indices that Seligsohn calculated, but rejected because he felt they failed to vary with diet in the manner predicted. From his histograms, it appears to me that they vary with diet to the same degree and in the same way as do indices VI, VII and VIII. They are:

- XXVI: height of protoconid / width of protoconid
- XXVII: height of protoconid / square root of: m2 length x m2 width
- XXVIII: height of protoconid / width of labial portion of m2

Values for each of indices VI-VIII and XXVI-XXVIII should be distributed such that insectivores score highest, some folivores³ next-highest, stem-eaters next, most folivores⁴ next and frugivores last. The same pattern should emerge with a plot of the average scores for these six indices. Naturally, this is true of Seligsohn's data.

4.2.2 My replication of Seligsohn's method

To test Seligsohn's method against the results of my food-breakdown experiment, I applied his method to seventeen species of extant and extinct primates (one pair of specimens for each species). These specimens were later used in my food-breakdown experiment. I scored each species for each of the seven aforementioned indices (Table 4-1). Species examined were ranked according to their index scores and predictions about diet were made in the same manner as in Seligsohn, 1977 (p. 36).

Raw data, in millimetres, are converted to the format in Table 4-1 using the following equation:

$$x_f = 100(x_i / \text{mean of } x_i) \quad (4-1)$$

where x_f is the final value appearing in a single cell of Table 4-1, and x_i is the initial measured value for that cell. For index XXXV, x_f is divided by 90 - a purely arbitrary number - to facilitate comparison with other histograms.

Figure 4-3 shows a histogram of the averages of indices VI-VIII and XXVI-XXVIII for all species measured. Species are ordered from bottom to top according to their scores. Extant species are used as guides for splitting all species into dietary groups and the pattern suggested by Seligsohn is also used to predict dietary preferences of extinct species. Species at the bottom of the diagram are predicted to be insectivores, those at the top are predicted to be frugivores and folivores should fall in between. The distribution of extant species on the histogram can be used to delimit categories of dietary inference (e.g., insectivores, frugivores).

Loris tardigradus and *Tarsius spectrum* are known to be highly insectivorous and moderately carnivorous (Napier and Napier, 1967; Chivers and Hladik, 1980; Jablonski and Crompton, 1994; Crompton *et al.*, 1998). *Nycticebus coucang*, though not well-studied, is thought to be an omnivore that consumes mostly insects, but some small vertebrates and fruit as well (Elliot and Elliot, 1967; Napier and Napier, 1967; Hladik, 1979). *Tupaia glis* consumes mostly insects but also some fruit (Napier and Napier, 1967; Emmons, 1991). All extinct species that fall below the lowest extant insectivore (*N. coucang*) on Figure 4-3

³ Those that possess specialized shearing crests (e.g., indris)

⁴ Those that do not possess specialized shearing crests (e.g., *Lemur catta*).

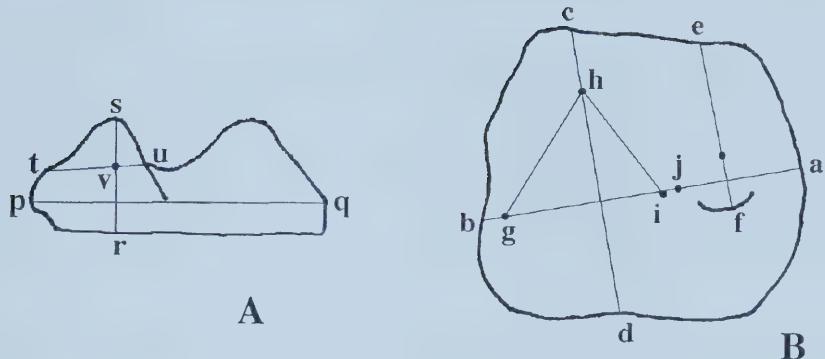


Figure 4-2 Sketches for Seligsohn's indices XXVI-XXVIII and XXXV. Both are drawings of the left m2 of the test specimen of *Notharctus sp.*. A, labial view (dorsal is up, anterior is to the left). p is the most mesial point on the tooth crown in labial view; q is the most distal point. r-s is perpendicular to p-q and connects the apex of the protoconid (s) to the cemento-enamel junction (r). t is the most ventral point on the mesial slope of the protoconid; u is the junction between the distal slope of the protoconid and the cristid obliqua. t-u is the width of the protoconid. v-s is the height of the protoconid. B, occlusal view (anterior is to the right, labial is up). a-b is a line through the most ventral point on the postcristid (g) and the most ventral point on the protocristid (j); a-b is the length of the m2. c-d is perpendicular to a-b, is drawn through the apex of the hypoconid (h) and is the width of the m2. e-f is parallel to c-d, is drawn through the lingual limit of the protoconid and the apex of the protoconid; e-f is the width of the labial portion of the m2. i is the terminal point of the cristid obliqua; g-h-i is the angle between the postcristid and the cristid obliqua.

are inferred to have been insectivores. *Otolemur crassicaudatus* eats primarily gum, insects and fruit (e.g., Cordell, 1991); all extinct frugivores should plot above *O. crassicaudatus* on Figure 4-3. *Lemur catta*, however, is a folivore-frugivore (Kay *et al.*, 1978; Ganzhorn, 1986; Yamashita, 1996) and it plots between the frugivores and the insectivores. Indices VI-VIII and XXVI-XXVIII from Seligsohn (1977) are good predictors of diet for the extant test species as the extant insectivores plot low on Figure 4-3 and the folivore and quasi-frugivore (*O. crassicaudatus*) respectively, plot above them.

Figure 4-4 shows a similar histogram for index XXXV. *Lemur catta*, the folivore-frugivore, plots very low on the histogram and *O. crassicaudatus* plots below it with the

highest score of all. Seligsohn predicted that leaf-eaters would score highly. However, frugivores should plot between insectivores and folivores. Considering the high scores of known insectivores (e.g., *Loris tardigradus*, *Tarsius spectrum* and *Nycticebus coucang*), there is not much room for frugivores. Therefore, this index is a poor predictor of diet for the extant test species.

These measurements may not entirely reflect the patterns shown by Seligsohn's own data because I used but one pair of specimens for each species, whereas Seligsohn measured between one and four pairs of specimens. Results of the comparison between these measurements and experimental food-breakdown data are given in Chapter 8. A strong correlation between the two would support the value of Seligsohn's technique for inferring diet.

	VI	XXVI	VII	XXVII	VIII	XXVIII	MEAN	XXXV
<i>Arapahovius gazini</i>	111	93	105	102	91	114	103	107
<i>Cantius eppsi</i>	87	92	85	86	88	73	85	101
<i>Carpodaptes hazelae</i>	73	114	61	68	68	54	73	104
<i>Carpolestes dubius</i>	92	92	106	101	125	113	105	101
<i>Lemur catta</i>	68	71	101	96	117	113	94	121
<i>Loris tardigradus</i>	143	126	135	148	126	132	135	111
<i>Notharctus sp.</i>	74	78	78	78	103	70	80	74
<i>Nycticebus coucang</i>	98	76	109	114	93	109	100	118
<i>Otolemur crassicaudatus</i>	89	85	104	106	92	81	93	124
<i>Phenacolemur praecox</i>	157	95	151	133	165	142	141	98
<i>Plesiadapis churchilli</i>	68	105	60	56	76	72	73	105
<i>Plesiadapis fodiatus</i>	104	86	94	89	91	90	92	81
<i>Plesiolestes problematicus</i>	113	128	99	111	118	124	116	100
<i>Smilodectes gracilis</i>	78	75	73	78	87	78	78	87
<i>Tarsius spectrum</i>	95	107	102	108	92	134	106	112
<i>Tetonius matthewi</i>	101	85	99	103	86	90	94	87
<i>Tupaia glis</i>	117	162	138	118	99	123	126	90

Table 4-1 Results of my replication of Seligsohn's method. Values are given as percentages of the mean for that index ($100 \times \text{value} / \text{mean}$). Values below 100 are thus below the mean for that index. The 'mean' column is the mean of all indices except XXXV. Raw values for index XXXV are divided by ninety.

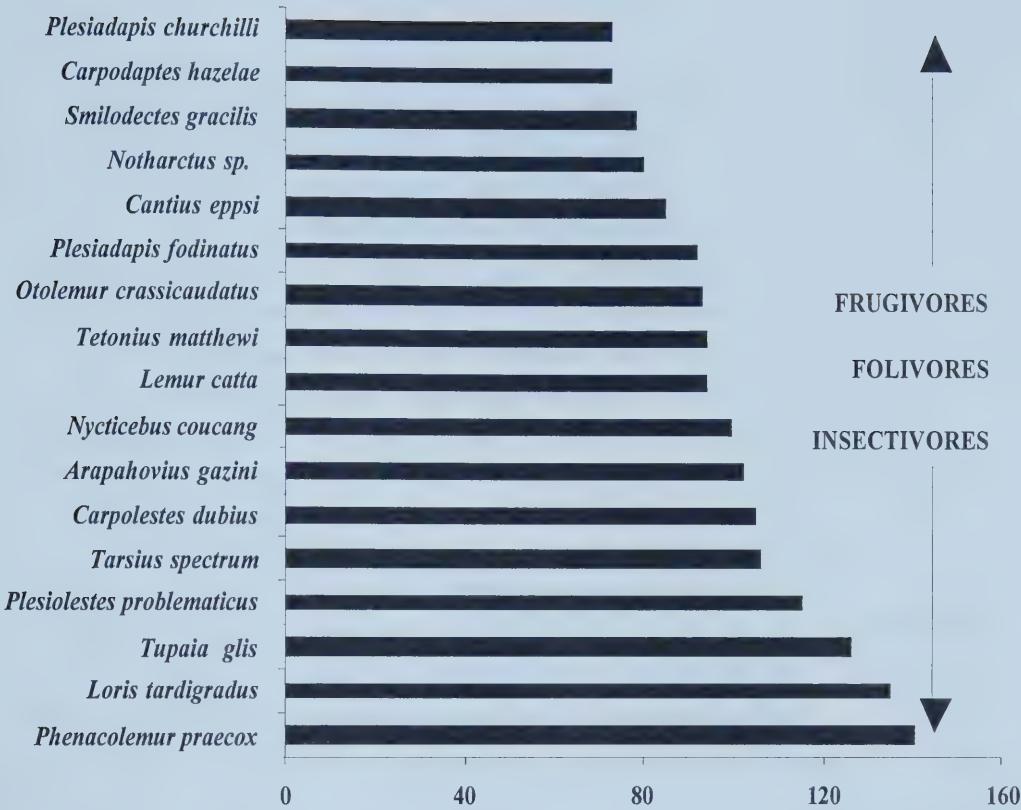


Figure 4-3 Mean of indices VI-VIII and XXVI-XXVIII from Seligsohn, 1977. Values are expressed as percentages of the mean.

4.3 Kay's method

4.3.1 Kay, 1975

Kay (1975) measured six features on the upper and lower second molars of several extant primate species. He then performed a principal components analysis⁵ on the measured values. He compared the variance in his Factors 1 and 2 to the various dietary preferences exhibited by the primates examined.

⁵ A principal components analysis, or p.c.a., is a method whereby several variables are examined for correlation and using these correlations, are reduced to a few composite variables.

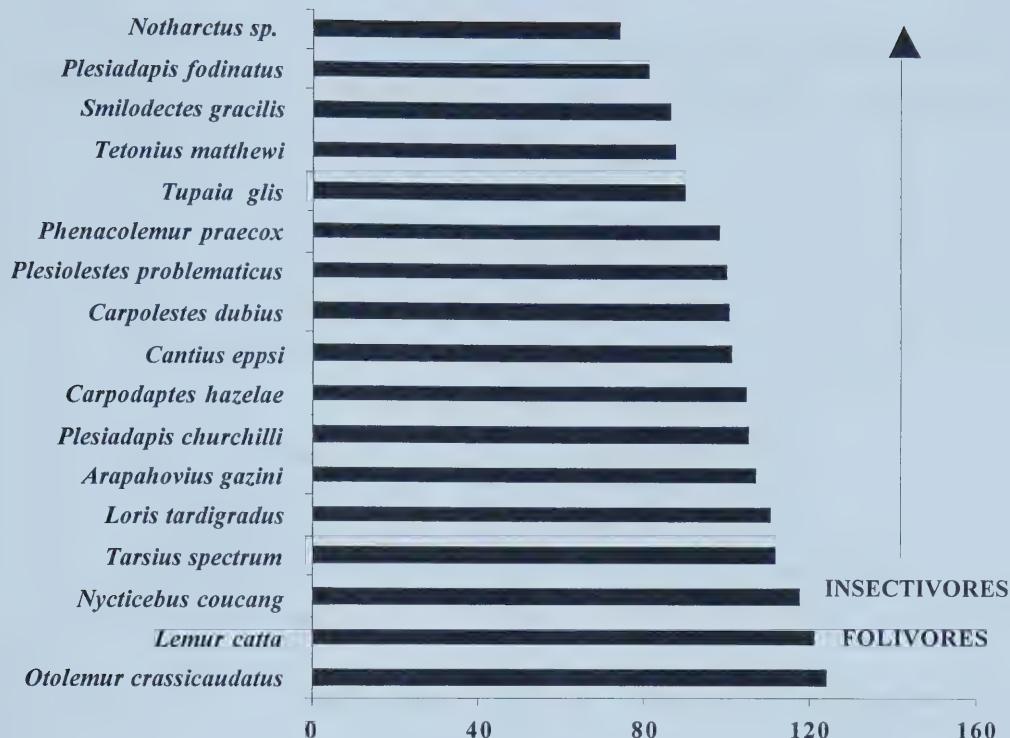


Figure 4-4 Scores for index XXXV. Raw values are divided by 90 and then the percentage of the mean is calculated. Values above are percentages of the mean. own data because I used but one pair of specimens for each species, whereas Seligsohn measured between one and four pairs of specimens. Results of the comparison between these measurements and experimental food-breakdown data are given in Chapter 8. A strong correlation between the two would support the value of Seligsohn's technique for inferring diet.

From his principal components analysis, Kay determined that his Factor 1 (that which represented the greatest percentage of the variance in his data) segregated frugivores (having low scores) from folivores and insectivores (having high scores). He admits that his method fails to segregate insectivores from folivores (p. 209), but that they can be separated based on size.

4.3.2 My replication of Kay's method

I replicated Kay's morphometric method for the seventeen species in my study. With the aid of an ocular micrometer, mounted on a binocular microscope, I measured the following dimensions on the lower second molar:

- Maximum mesio-distal length of the m2.
- Length of the cristid obliqua.
- Crown height at the hypoconid. This is the distance, in the vertical plane, from the tip of the hypoconid to the ventral most reach of the cemento-enamel junction at the base of the m2.

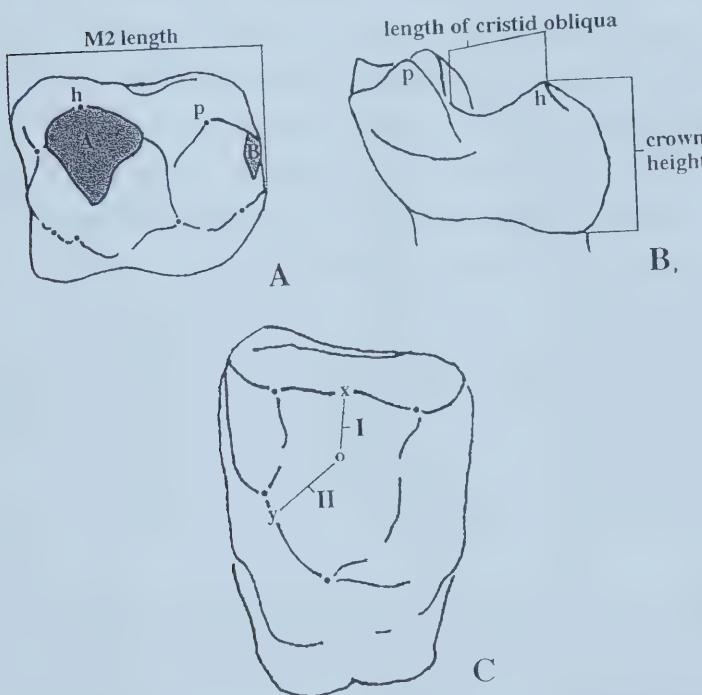


Figure 4-5 Sketches showing Kay's six initial measurements. Modified from Kay, 1975. All depict left molars of *Pelycodus (?Cantius) ralstoni*. A, m2 in occlusal view (anterior is to the right, labial is up). h is the hypoconid, p is the protoconid. Area A and area B represent the total area for crushing and grinding. B, m2 in labial view (anterior is to the left, dorsal is up). h is the hypoconid, p is the protoconid. C, M2 in occlusal view (anterior is to the left, labial is up). x is the most dorsal point on the centrocrista, o is the deepest point in the trigon basin, y is the most dorsal point on the preprotocone crista, P is the paracone, M is the metacone and Pt is the protocone. Distance I represents the length of the Phase I traverse (i.e., the path of the hypoconid during Phase I of mastication); distance II represents the length of the Phase II traverse.

Using the same equipment, I then measured the following dimensions on the upper second molar:

- Length of the Phase I traverse. This is the distance between the ventralmost point of the centrocrista and the ventralmost point of the trigon basin.
- Length of the Phase II traverse. This is the distance between the ventralmost point of the trigone basin and the end-point of the hypoconid's path of movement (on the mesio-lingual surface of the protocone).

Then, using a camera lucida mounted on the same microscope, I traced the outlines of the crushing and grinding surfaces on the m2. I digitized these and used 'MacMeasure II' to calculate their areas. Summed, these areas constitute the last measurement:

- Area of crushing and grinding surfaces.

Table 4-2 shows the values for these six measurements for the species I studied.

Note that only one pair of specimens was used for each species. Raw data in millimetres (or millimetres squared) for all species are converted into natural logarithms, that are plotted against natural logarithms of body mass (from Fleagle, 1999) in an x-y scatterplot. One scatterplot is generated for each of the six measurements. Each of the seventeen species constitutes a series on the scatterplot (plotted with \log_e body size on the x-axis as the independent variable). A first-order polynomial of the format $y=mx+b$ is fitted to each series using a least-squared regression ('trendline' command in 'Microsoft Excel 5.1').

Species A is removed from the data matrix and the corresponding scatterplots. This changes the equation for the regression line on each plot. The natural logarithm for the body mass of species A is substituted into the new equation for each of the six plots (as the x-value) and the y-value - or *predicted* value - for each of the six measurements is calculated for species A.

The predicted value is then compared to the observed value to calculate the percentage difference between the two:

$$\text{percentage difference} = 100 \times ((\text{observed} - \text{expected}) / \text{expected}) \quad (4-2)$$

The percentage difference is the value that appears in Table 4-2.

Species A is returned to the data set. Then species B is removed and the same values are calculated for B, and so on (Kay, 1975, p.199).

The values of percentage difference are then fed into a principal components analysis ('factor analysis' in 'SPSS 10.0 for Windows'). Those three factors that account for most of the variance in the data are listed in Table 4-2 as Factors 1 through 3. The percentage of variance represented by each factor and the component matrix are given in Table 4-3.

Factors 1 and 2 are plotted against one another in Figure 4-6. Factors 1 and 3 are plotted against one another in Figure 4-7. Factors 2 and 3 are plotted against one another in Figure 4-8. Roughly speaking, Factor 1 represents brachydonty (a high score represents a low, small tooth with lots of shearing and grinding surface), Factor 2 represents amount of shear, and a high score for Factor 3 represents a tall, grinding tooth with little transverse shear.

species	A	B	C	D	E	F	Factor 1	Factor 2	Factor 3
<i>Carpodaptes hazelae</i>	-36.2	19.7	-635.0	51.9	108.5	-2.2	1.5348	-1.5287	-2.2871
<i>Tarsius spectrum</i>	36.7	-85.4	81.8	-38.0	-151.1	-75.9	-1.2138	0.1873	0.4578
<i>Carpolestes dubius</i>	-45.6	122.9	-141.2	194.5	127.5	190.4	1.3556	-0.3985	-0.4545
<i>Plesiolestes problematicus</i>	13.6	-149.8	-24.1	-52.2	-109.1	45.8	-0.7958	-0.2717	-0.2895
<i>Tetonius matthewi</i>	-6.6	60.3	8.0	-28.6	210.2	-51.5	0.0272	0.0713	-0.1039
<i>Tupaia glis</i>	35.1	-29.0	160.6	-136.2	-269.3	-149.7	-1.2905	0.3773	0.6785
<i>Loris tardigradus</i>	29.3	-122.1	49.7	-124.4	69.4	-106.7	-1.2120	0.0664	-0.0358
<i>Arapahovius gazini</i>	-19.0	201.8	-56.3	1163.2	25.4	257.0	1.9846	0.0004	1.9568
<i>Phenacolemur praecox</i>	-9.2	113.2	-48.7	227.1	-3761.1	1654.6	0.6695	-0.6500	1.8955
<i>Plesiadapis fodinatus</i>	3.2	223.7	73.5	6.7	3031.3	5076.1	0.8254	3.4323	-1.1039
<i>Nycticebus coucang</i>	3.2	-393.5	-60.4	-42.9	-157.4	-68.9	-1.1383	-0.9390	-0.9264
<i>Plesiadapis churchilli</i>	1.6	52.4	-28.5	132.8	-330.3	-33.8	0.0827	-0.1355	0.3792
<i>Cantius eppsi</i>	-10.6	-42.3	-15.8	-2.1	-100.0	-141.3	-0.0969	-0.3363	-0.2210
<i>Otolemur crassicaudatus</i>	-4.0	-14.3	4.8	-39.5	15.1	-0.3	-0.2001	-0.0933	-0.1624
<i>Smilodectes gracilis</i>	-1.9	37.4	-1.7	-27.2	42.5	38.8	-0.0861	0.0291	-0.0559
<i>Lemur catta</i>	12.7	26.0	16.7	16.1	-94.4	-20.0	-0.3611	0.0947	0.2758
<i>Notharctus sp.</i>	-3.4	32.9	25.5	-5.0	138.6	51.4	-0.0854	0.0943	-0.0029

Table 4-2 Values from my replication of Kay's method. A-F are expressed as Log_e percentage differences (100 x (value-mean)/mean). Factors 1-3 are from my principal components analysis. A: maximum mesio-distal length of m2, B: true length of cristid obliqua, C: crown height at hypoconid, D: total area of crushing and grinding, E: length of phase I traverse, F: length of phase II traverse.

4.3.3 Dietary predictions made using Kay's method

The following interpretations are based on Figures 4-6 and 4-7. Each of the first two graphs expresses more than 50% of the variation in the six initial measurements, whereas Figure 4-8 expresses about 45%.

Tupaia glis, *Tarsius spectrum*, and *Loris tardigradus* plot on the far left. These species are all mainly insectivorous or carnivorous, though *T. glis* often consumes fruit (e.g., Chivers and Hladik, 1980; Langham, 1982; Emmons, 1991). These species also share a large, high crowned m2's with short shearing crests and little grinding surface. Short

	Component Matrix		
	Factor 1	Factor 2	Factor 3
max. length m2	-0.85	0.31	0.24
cristid obliqua length	0.74	0.44	0.28
crown height	-0.57	0.54	0.53
total grinding area	0.69	-0.07	0.53
phase I traverse	0.06	0.66	-0.56
phase II traverse	0.32	0.80	-0.10
Eigenvalues			
% variance explained	Factor 1	Factor 2	Factor 3
	36.43	27.64	17.16

Table 4-3 Output for principal components analysis. Original variables are in the left-hand column. Factors 1-3 explain most of the variance in the six original variables (total = 81.23%).

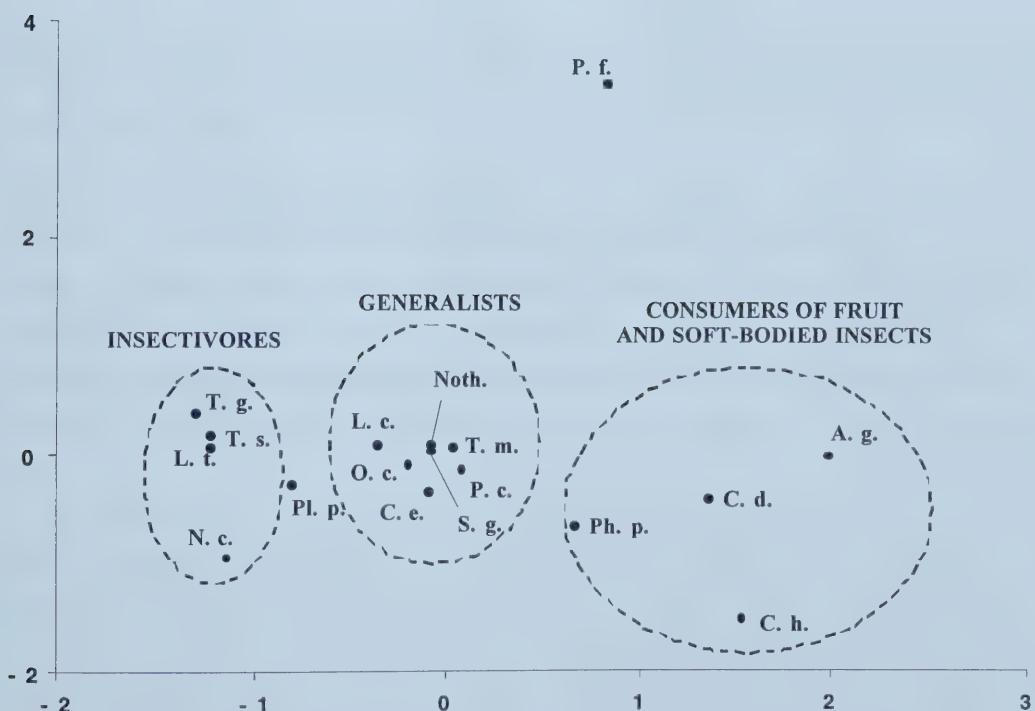


Figure 4-6 Factor 2 plotted against Factor 1. See text for description and Appendix 1 for species names abbreviated here. X-axis: Factor 1 (brachydonty); y-axis: Factor 2 (shear).

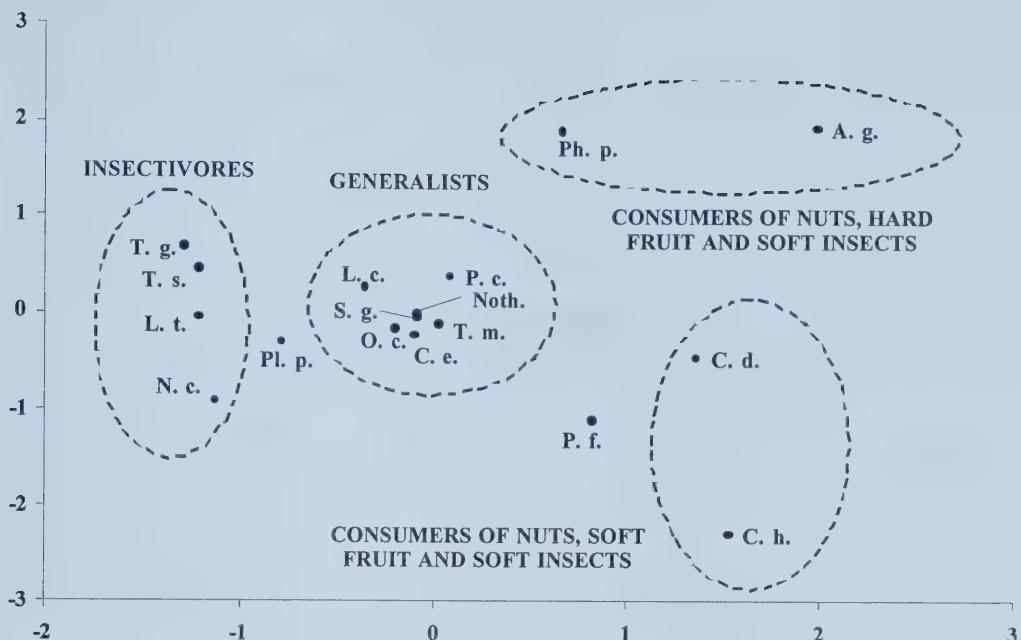


Figure 4-7 Factor 3 plotted against Factor 1. See text for description and Appendix 1 for species names abbreviated here. X-axis: Factor 1 (brachydonty); y-axis: Factor 3 (crown height, grinding area).

shearing crests, along with high-crowned, large molars, have been suggested as adaptations to feeding on adult insects (Kay, 1975; Strait, 1993). Such insects have cuticles that are “tough, stiff, strong and subject to brittle fracture” (Strait, 1997, p.204). To cause such a material to shatter, such that the nutritious contents might be expressed, a short shearing blade is better than a long one because pressure increases as the area of the point of contact decreases. The highly insectivorous extant species in this study possess very short shearing blades.

In both figures *Nycticebus coucang* plots below and to the right of the highly insectivorous group. As mentioned above, slow lorises eat mostly insects, though they consume fruit and perhaps small birds (Elliot and Elliot, 1967; Napier and Napier, 1967; Hladik, 1979). This species possesses smaller molars with less vertical shear than those of the aforementioned insectivores. This analysis suggests that the molars of *N. coucang* are less adapted to insectivory and perhaps slightly more adapted to frugivory than are the molars of *Tupaia glis*, *Tarsius spectrum* and *Loris tardigradus*. Frugivores are thought to possess smaller molars (relative to body size) with less vertical shear than we see in insectivores and folivores (Kay, 1975). *Plesiolestes problematicus* plots near to *Nycticebus*

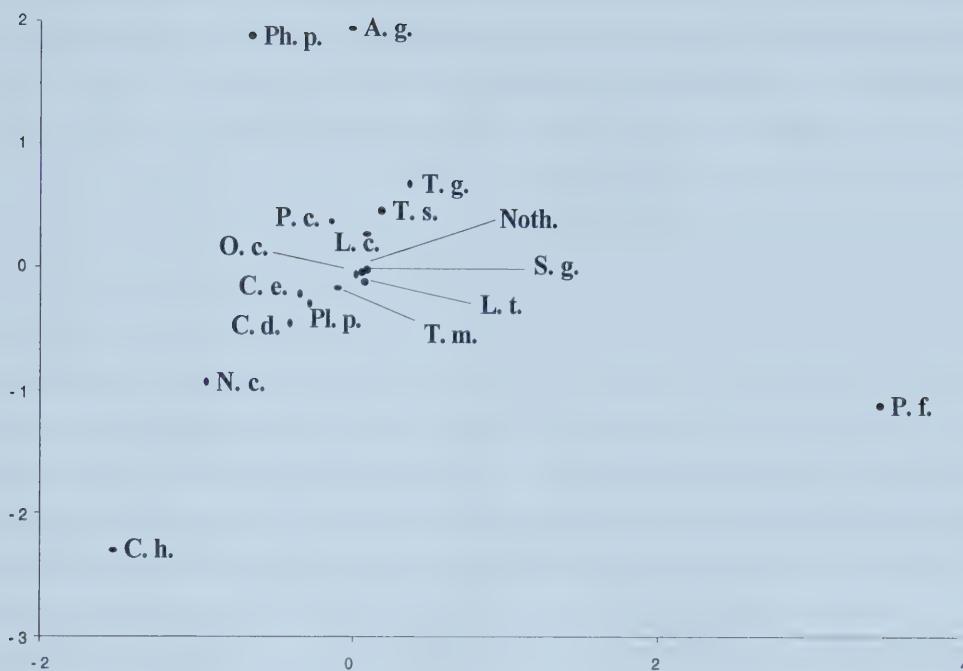


Figure 4-8 Factor 3 plotted against Factor 2. See text for description and species names abbreviated here. X-axis: Factor 2 (shear); y-axis: Factor 3 (crown height, grinding area).

coucang in both figures and its molars are similar in the dimensions measured. Therefore, it may be reasonable to infer a similar diet for this fossil species: mostly insects, perhaps some small vertebrates, and some fruit.

Seven of the test species plot around the origin. These are: *Lemur catta*, *Otolemur crassicaudatus*, *Smilodectes gracilis*, *Cantius eppsi*, *Notharctus sp.*, *Tetonius matthewi* and *Plesiadapis churchilli*. These species all possess moderately sized molars, with modest amounts of shearing and grinding and shearing crests of medium length. *Lemur catta* eats mostly leaves and fruit (e.g., Kay *et al.*, 1978). *Otolemur crassicaudatus* eats large quantities of gum and variable quantities of insects and fruit (e.g., Cordell, 1991). These extant species and these five extinct species may be considered dietary generalists, i.e., the molars are not adapted to one specific kind of food but are useful for breaking down several kinds.

Occupying a position at the lower right-hand side of Figure 4-6 is a group of four species: *Phenacolemur praecox*, *Carpolestes dubius*, *Carpodaptes hazelae* and

Arapahovius gazini. These species all possess low crowned, small m2's with long shearing crests and a large area for grinding. Figure 4-7 separates this group into two (or three) groups based on the very small size of the carpolestid molars and the much larger grinding area in the other two species. *Phenacolemur praecox* is separated from *Arapahovius gazini* based on its very small amount of vertical shear capacity and its very large capacity for horizontal shear (both measured on the M2). Long shearing crests are particularly useful for dividing soft-bodied invertebrates such as caterpillars, moths and worms that are “fragile, pliant, weak, and ductile” (Strait, 1997, p.204). To be fragmented, these food items must be penetrated repeatedly by a sharp blade. Another kind of food that possesses these material properties is soft fruit or semi-hardened gum (personal observation). The possession by the carpolestids, *P. praecox* and *A. gazini* of long shearing blades suggests they may have been eating soft-bodied invertebrates or soft fruit. As the latter two species possess a much greater capacity for grinding, perhaps they were additionally consuming some harder fruits or seeds. Alternately, they may have possessed stomachs able to digest chitin and they were breaking down insect cuticles during mastication. The molars of *P. praecox*, in particular, possess little capacity for vertical shear. However, based on measurements adapted from Kay (1975), this species possessed an enormous capacity for horizontal shear. This suggests it was grinding and shearing thin sheet-like materials, such as insect cuticle, leaves, or seed shells.

Plesiadapis fodinatus plots in a somewhat enigmatic fashion. This is largely due to its extremely high capacity for both horizontal and vertical shear. It is possible that it fed on foods that were thick and ductile, yet fibrous, such as the shoots or stems of young plants.

Values for the six basic measurements are compared in Chapter 8 to values for experimental food-breakdown. Food-breakdown is also compared to the results of the principal components analysis to determine whether or not there is a correlation. A strong correlation would support the value of Kay’s technique for inferring diet. Furthermore, any similarity between the dietary inferences made here and those made from the results of the chewing experiment would strongly support both methods of inference. Any differences would suggest that one or the other method must be re-examined as to its usefulness.

4.4 Evans and Sanson’s method

4.4.1 Tip sharpness and cusp sharpness

Currently, it is very popular to infer diet from the sharpness of cusps. Although cusp sharpness is easily assessed qualitatively, it can also be quantified to test for a

correlation between sharpness and diet. Lucas (1982) pioneered a method whereby the sharpness of the tip of a cusp is quantified. The sharpness of the tip of a cusp is proportional to *radius of curvature* at the tip of that cusp. This can be measured in several different ways, but it is easiest to conceive of as the radius of the smallest circle that can be fit into the tip of the cusp (Yamashita, 1998).

At this point, it is necessary to define ‘cusp’. A cusp is a parabolic feature on a tooth for which a function fitted to its outline has a single local maximum⁶, and is bounded by a local minimum⁷ at either side on its base. Thus, it is basically shaped like a parabola. This definition does not work for cusps that are distinctly non-parabolic.

Tip sharpness is especially important for diet because it gives an estimate of the area of contact between the tooth and an item of food (Evans and Sanson, 1998). Why is the area of contact important? The smaller the area of contact between the tooth and the food, the more concentrated the forces resulting from contraction of the masticatory muscles will be. The sharper the tip of a cusp, the easier it will be for that cusp to puncture food. This is particularly important when the food is brittle because once a brittle material is punctured, cracks propagate through it causing rapid fragmentation (Strait, 1997).

Related to the concept of tip sharpness is the concept of *cusp* sharpness. ‘Cusp sharpness’ is defined as “the volume or surface area of the cusp at increasing distances from the tip” (Evans and Sanson, 1998, p.392). The sharpness of a cusp has little influence of the breakdown of brittle foods - these fragment as soon as they are punctured. However, ductile foods are better fragmented by a cusp with a smaller volume than by a cusp with a larger volume. A cusp can be seen as a wedge driven into food: a cusp with a large volume will have a greater angle (measured at the tip, along opposite sides) than a cusp with a small volume. As the cusp penetrates a ductile food, the food will act like a viscous liquid and surround the cusp tip. The more hydrodynamically shaped cusp (i.e., the more acute-angled one) will move through the food with greater ease.

Evans and Sanson (1998) argued that a cusp with a sharp tip will fragment a brittle food with ease, whereas a sharp cusp (i.e., less volume at a given distance from the tip) will fragment a ductile food with ease. They also suggested, *contra* Strait (1993, 1997), that hard-bodied insects, like beetles, do not fracture as soon as the cuticle is breached, but rather a cusp must also be driven clear through the insect to achieve effective fragmentation. The insides of such insects are generally ductile while the cuticle is brittle; therefore, the best

⁶ A local maximum is a point of inflection at which the derivative of the function x ($f'(x)$) is equal to zero and the double derivative of the function x ($f''(x)$) is smaller than zero (Stewart, 1995).

⁷ A local minimum is a point of inflection at which $f'(x)=0$ and $f''(x)>0$ (Stewart, 1995).

cusp for processing hard-bodied insects is one with a sharp tip and a small volume (Evans and Sanson, 1998).

4.4.2 Evans and Sanson, 1998

Evans and Sanson (1998) tested the above hypotheses by conducting an experiment. They fashioned several ‘punches’ of different tip and cusp sharpnesses. They then drove the punches through adult and larval specimens of *Tenebrio sp.* (a beetle) and measured the amount of force necessary to 1) penetrate the cuticle, and 2) punch through to the other side of the body. They found that, indeed, it takes less force for a sharp tip to penetrate the cuticle and it takes less force for a sharp cusp to punch through the body.

In order to measure tip and cusp sharpness, it was necessary for Evans and Sanson (1998) to calculate the radius of curvature of each ‘cusp’. This was achieved by fitting a second-order polynomial to the outline of each cusp. Tip sharpness is the minimum radius of curvature for a cusp. The equation for the fitted polynomial ($f(x)$) is then inserted into the following formula to determine radius of curvature:

$$\text{minimum radius of curvature} = (1 + (f'(x))^2)^{3/2} / f''(x) \quad (4-3)$$

where $f'(x)$ is the derivative of $f(x)$ and $f''(x)$ is the derivative of $f'(x)$

To calculate volume, each cusp was modeled as a paraboloid and an equation was fitted to each. Volumes at 0.5mm and 3mm from the tip were calculated by using 0.5 and 3 respectively as the height (y) of the paraboloid.

The equation for the volume of a paraboloid is

$$\text{Volume} = \pi \times \text{the integral of } f(x) \text{ (from 0 to } y) \quad (4-4)$$

where y is distance from the tip in millimetres.

This can also be expressed as follows:

$$\text{Volume} = \pi \int_0^y f(x) dx$$

Evans and Sanson suggested that if volume is plotted against height (i.e., distance from the tip), the slope will be greater for blunter cusps (see Evans and Sanson, 1998, Figure 2.). This is because they defined cusp bluntness as the volume of a cusp relative to the height of the cusp.

4.4.3 My replication of Evans and Sanson’s method

I calculated the tip sharpness and cusp sharpness for all premolar and molar cusps for all the species I tested. However, cusp number varies tremendously between these

species - especially on the premolars. Therefore I included only four cusps in my final analysis. These are the M2 paracone, the M3 protocone, the m2 protoconid and the m3 hypoconulid. These were chosen because they were present on all specimens and because their homologies are relatively certain in the taxa I tested.

The method for calculating tip sharpness and cusp sharpness on fossil specimens (as opposed to artificial cusps *à la* Evans and Sanson) is complex. Using a camera lucida attached to a binocular microscope, I drew the outline of each cusp. To maintain consistency, a cusp was always drawn in the same view. The M2 paracone, the m2 protoconid and the m3 hypoconulid were always drawn in labial view, whereas the M3 protocone was always drawn in lingual view. It was difficult to consistently draw cusps in the same orientation. This is because some cusps are asymmetrical, ‘leaning’ to one side or another - unlike a perfect parabola that has a midline dividing it into mirror images. To compensate for this asymmetry, I aligned each cusp such that its tip pointed directly upwards. The distance from the imaginary midline to either side of the cusp outline (at the base of the cusp) was kept equal.

Next, I digitized the outline drawings of all cusps using a digitizing tablet and the digitizing software package, ‘MacMeasure II’. Cusp outlines were digitized as x-y scatters. These were then imported into ‘Microsoft Excel 5.1’ and converted to x-y scatterplot graphs. A second-order polynomial was then fitted to the scatter for each cusp using the ‘trendline’ command. The equation for each cusp ($f(x)$) was inserted into the equation 4-3 to calculate minimum radius of curvature at the tip of that cusp. Minimum radius of curvature is equivalent to the inverse of tip sharpness.

Using height values from 1mm to 10mm, I calculated cusp volume for the same cusps. Cusp volume is equivalent to the inverse of cusp sharpness.

Figure 4-9 is a histogram that shows the mean minimum radius of curvature for each species tested. The mean for each species is simply the mean of the values for the four selected cusps. The higher the value, the blunter the cusp tip.

Figure 4-10 is an x-y scatterplot of means cusp volume plotted against distance from the tip (i.e., height). Purely for the sake of convenience, lines were drawn through the points for each series. Mean cusp volume is simply the mean of the volumes of the four selected cusps. The greater the slope of the line, the blunter the cusp.

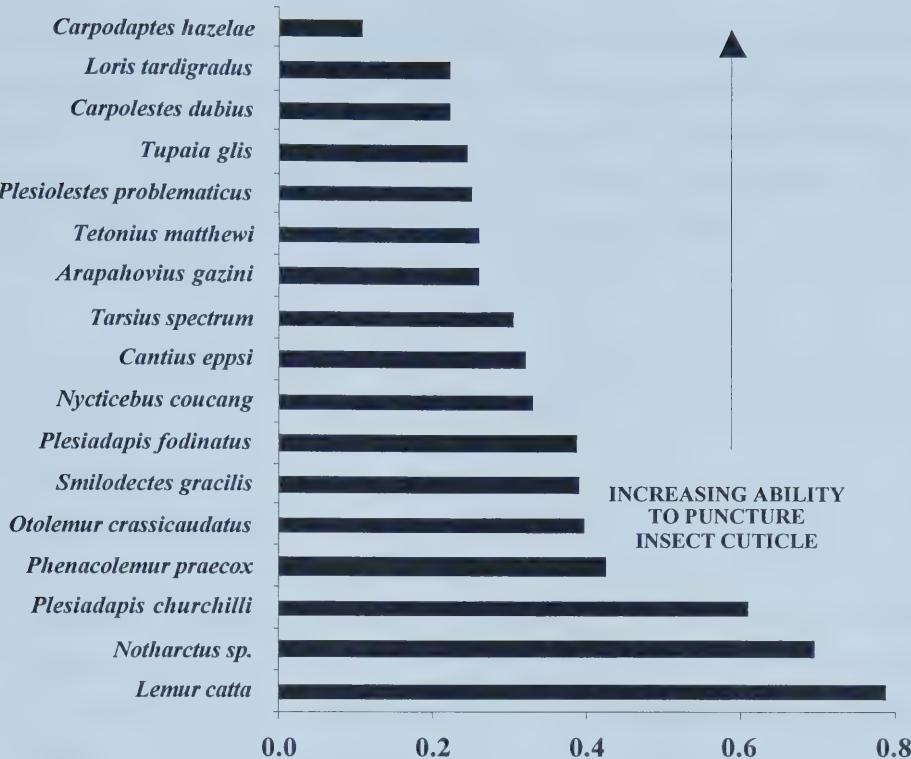


Figure 4-9 Mean minimum radius of curvature for four selected cusps. Values are in millimetres. High values are for blunter cusps (e.g., *Lemur catta*).

To estimate the amount of measurement error incurred by this method, I traced a single cusp 30 times using the camera lucida. I then digitized each of the 30 tracings and plotted a second-order polynomial trendline for each. Minimum radius of curvature was then calculated for each of the 30 polynomials. The average percent error among the 30 values is 4.0%, with a range of 0.096% to 9.8%. Percent error was calculated using the following:

$$100 \times (\text{observed value} - \text{expected value}) / \text{expected value} \quad (4-5)$$

where the expected value is simply the mean of the observed values.

Evans and Sanson (1998) relate tip sharpness and cusp sharpness to the effectiveness of breaking down insects. Therefore, Figures 4-9 and 4-10 provide the basis for predictions about how well the test species break down insects. The ranking of species in Figure 4-9 suggests that the carpolestids, *Loris tardigradus* and *Tupaia glis* penetrate insect cuticle effectively. Whereas *Lemur catta*, *Notharctus sp.* and *Plesiadapis churchilli* penetrate insect cuticle ineffectively. All other species fall in between. Species rank somewhat differently with respect to cusp volume (Figure 4-10). These differences suggest that some species are well-adapted to penetrating insect cuticle (or similar materials) but

poorly adapted to punching through insect bodies (or similar materials), or vice-versa. For example, *Tarsius spectrum* has molar cusps that appear to be effective for punching through insect bodies, but less-effective for penetrating them. Perhaps *T. spectrum* uses its premolars or canines to penetrate insect cuticle (see Jablonski and Crompton, 1994). By contrast, *Loris tardigradus* and *Carpolestes dubius* possess molars that appear to be effective for penetrating hard insect cuticle, but less effective for punching through their bodies.

As for Seligsohn's method and Kay's method, the results of my replication of Evans and Sanson's method are compared to the results of my chewing experiment. These comparisons are in Chapter 8.

4.5 Limitations and reservations

Because "the shape of a tooth or cusp cannot be quantified by a single number or ratio" (Evans and Sanson, 1998, p. 392), the above three methods for measuring molars to infer diet, as well as all other conceivable methods, are simplifications. Each method quantifies one or a few aspects of molar morphology. The whole dentition (especially the molars and premolars) is partly shaped by the properties of food; therefore, diet should not be inferred from one measurement alone. However, if dietary inferences are to be made, they should be based on some part of the morphology that can be measured feasibly.

Seligsohn's method independently compares several features of primate molars to diet. This method has the advantage of examining several aspects of morphology, thereby increasing the chances of discovering one that correlates with food preference. It is also easy to use. Unfortunately, its predictions are rather vague, so it has questionable usefulness in paleontology.

Kay's method integrates measurements of a few primate molar features and compares the integrated pattern to diet. This method has the advantage of using several features. It is a bit more difficult to implement than Seligsohn's method and the results of the principal components analysis are somewhat difficult to interpret. If this method were applied to different mammalian groups, it is quite possible that the factors in the resulting principal components analyses would be different every time. Equally, it might result in factors that are uninformative (e.g., Factor II in Figure 4 and page 211 of Kay, 1975).

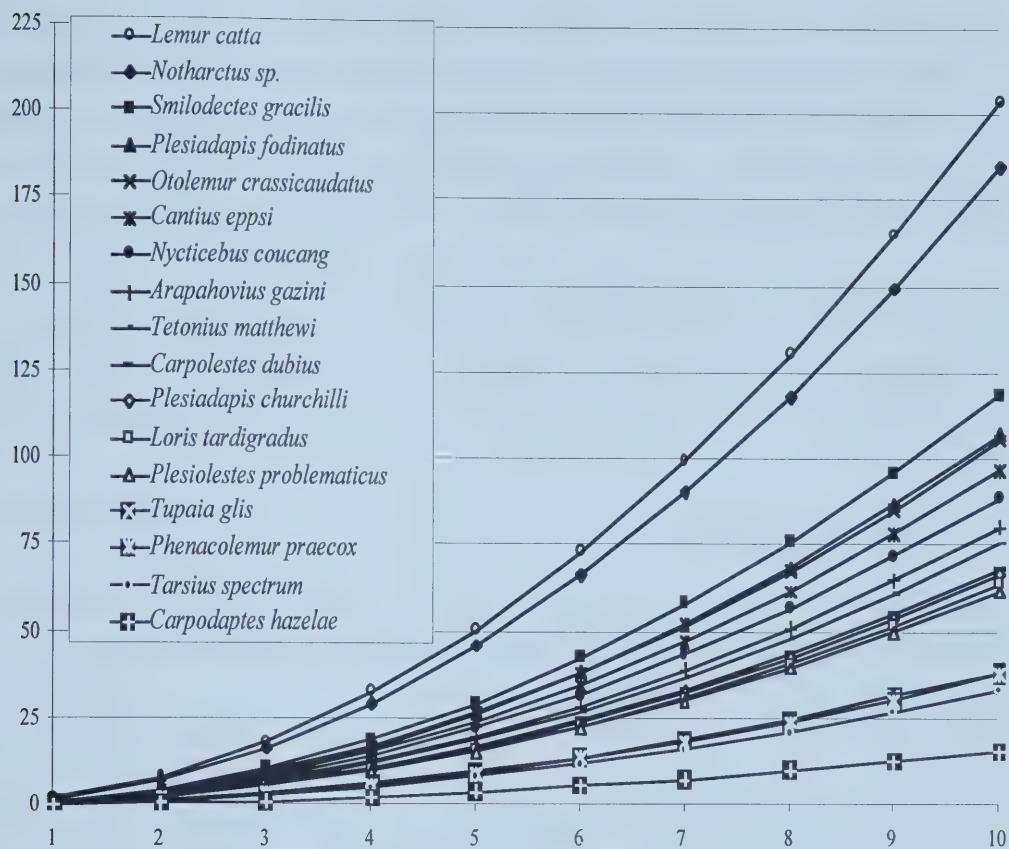


Figure 4-10 Mean cusp volume of four selected cusps plotted against distance from the tip. Cusp volume is measured in millimetres cubed (mm^3) and the distance from the tip is measured in millimetres. Species names are ordered to match the slopes of the lines. Species with blunter cusps have steeper lines (e.g., *Lemur catta*). X-axis: cusp height (mm); y-axis: cusp volume (mm^3).

Kay's method makes definite predictions about diet from molar morphology, but to compare a new taxon to those already analyzed, the new taxon must be added to the existing ones and the analysis must be run again. Unfortunately, with the addition of new taxa, the factors in the principal components analyses may change substantially, perhaps even reversing the original predictions.

Evans and Sanson's method (which could also be called Lucas's method (Lucas, 1982) or Yamashita's method (Yamashita, 1998)) is powerful because it generates distinct predictions. However, the resulting predictions may be insignificant because this method considers only one aspect of molar morphology. It may be that the cusp tips of the molars of a particular primate are particularly sharp and are therefore well-adapted to puncturing insect cuticle, but perhaps its molars also have very wide basins, adapted for pulping fruit.

One might draw the incautious conclusion that the primate in question is a specialized insectivore. Moreover, this method consists of a great number of steps. At each step, measurement errors could occur, and because of the number of steps, might add up to a significant error in the end. However, the test I performed to detect percent error suggests that Evans and Sanson's method is relatively error-free.

Each of these morphometric methods is but an approximation. Other methods exist and future students of the form-function relationship will generate new ones. In Chapters 8 and 9, the relative merits of these morphometric methods are weighed against each other and against masticatory performances.

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Chapter 5: Muscles of mastication

5.1 The modern analogue

I have chosen the thick-tailed bushbaby, *Otolemur crassicaudatus* as a modern analogue for mastication in all the species that I tested in the mastication machine. The machine was designed using the masticatory variables (e.g., muscle force and length of mastication cycle) of primarily this species. Most of these variables were well known prior to this study. However, it was necessary for me to estimate the force (during mastication) exerted by each masticatory muscle in *O. crassicaudatus*.

To study the behaviour of extinct taxa, paleontologists usually draw on analogues from within the extant biota. There are many kinds of analogues: behavioural analogues, morphological analogues, ecological analogues, etc. In an experimental study such as this one, the choice of a good modern analogue is paramount: the significance of all results depends on how well the analogue chosen represents the extinct taxa studied.

The search for modern analogues for the earliest primates has been extensive (e.g., Cartmill, 1974; Charles-Dominique, 1977; Sussman and Raven, 1978; Jablonski, 1986) and various taxa have been suggested. The common tree shrew (*Tupaia glis*) has been used by some (Abplanalp, 1971; Hiiemae and Kay, 1972, 1973; Kay and Hiiemae, 1974; Goode and Haines, 1975; Fish and Mendel, 1982), because of its superficial resemblance to plesiadapiforms and because it shares some features with primates in general. However, if a tree shrew is chosen as the modern analogue, perhaps it should be the feather-tailed tree shrew (*Ptilocercus lowii*) as this is the most primate-like of the tree shrews (Van Valen, 1965; Butler, 1980; Luckett, 1980). Most primatologists now believe that the features shared by primates and tree shrews are actually primitive retentions (e.g., Fleagle, 1999). However, phylogenetic proximity is not a prerequisite for functional analogy. Regardless of its taxonomic position, the tree shrew may still serve as a useful analogue for the earliest primates.

Maybe the Lemuriformes include the most primitive living primates. Accordingly, some lemurs (usually members of the family Cheirogaleidae) are considered modern analogues for the earliest primates (Fleagle, 1999). Several primatologists distinguish between the primitive condition of cheirogaleids (Lemuriformes: Cheirogaleidae) and the derived condition of lemurids (Lemuriformes: Lemuridae). Charles-Dominique (1977) suggested that lemurids are highly derived relative to the other African strepsirrhines: they possess several adaptations to a diurnal habitus (e.g., small orbits, large body size, folivory), whereas the earliest primates were likely nocturnal. He proposed that the dwarf or mouse

lemurs (Cieriogaleidae) and the galagos (Lorisiformes: Galagidae) share several features related to nocturnality and that both of these families are generally plesiomorphic relative to the highly diverse, diurnal Lemuridae. Based on similarities of the blood flow to the brain, the morphology of the basicranium and other synapomorphies (Cartmill, 1975; Szalay and Katz, 1973; Tattersall and Schwartz, 1975), cheirogaleids are sometimes considered closely related to Lorisiformes to the exclusion of the lemurids (Jablonski, 1986). Perhaps either Cieriogaleidae or Lorisiformes include the best analogues for the earliest primates.

Others (Charles-Dominique and Martin, 1985; Rasmussen and Nekaris, 1998) favour the use of specifically galagos as models for the masticatory behaviour of the earliest primates because of the probable similarities in mastication between these two groups.

There is little consensus as to which modern species should be used as a behavioural analogue for the earliest primates. This disagreement has two main sources: uncertainty or imprecision about what taxa constitute the ‘earliest primates’ and imprecision about what behaviour - or more precisely, what *physical action* - is being modeled.

Chapter 2 contains extensive discussion of the various opinions on what taxa constitute the earliest primates. If plesiadapiforms are considered the earliest primates, then perhaps a tree shrew is the best modern analogue. Whereas, if the omomyids and the adapids are considered the earliest primates, then perhaps a galagid or a cheirogaleid is the best modern analogue.

As for the question of what physical action is being modeled, my aim is to model mastication. It is unlikely that we will find an extant species that can be used as a modern analogue for *all* physical actions performed by the test species. Therefore, we must seek an extant taxon that is analogous with respect to a *single* action. Most of the earliest primates (be they plesiadapiforms, omomyids or adapids) are known from only isolated teeth and jaws with teeth, so the most fact-based action to study is mastication.

Jablonski (1986) considered the masticatory behaviour of several potential analogues for mastication in the earliest primates. She concluded that each grade in the early evolution of primate mastication can be represented by a different modern analogue. For example, she suggested that the “use of tree shrews as models for the study of occlusion and jaw movements in primitive eutherians (including primates)... is justified” (Jablonski, 1986, p. 541). However, she stressed the similarities between the masticatory complex in adapids and the masticatory complex in extant strepsirrhines. If the adapids are included within the ‘earliest primates’ then the tree shrew model proves somewhat inadequate.

Regardless of what fossil taxa should constitute the earliest primates, I am constrained in my choice of modern analogue by the fact that only one of the potential

analogues has been sufficiently studied as to its masticatory behaviour. That is the thick-tailed galago, *Otolemur crassicaudatus*.

5.2 The anatomy of the muscles of mastication in *Otolemur crassicaudatus*

5.2.1 Summary of the relevant literature

Mastication and the muscles responsible for it are well-studied in a few primate species. As for the anatomy of the masticatory muscles, humans are the most well-studied (e.g., Swindler and Wood, 1973; Aiello and Dean, 1990; Miller, 1991; Lang, 1995), though the anatomy of the masticatory muscles of macaques (Schwartz and Huelke, 1963; Anton, 1999), baboons (Swindler and Wood, 1973) and chimpanzees (Swindler and Wood, 1973) are documented also.

Although studies of the postcranial anatomy of galagids are common (Jablonski, 1986), studies of the masticatory complex are few. The first depiction of the muscles of mastication in a galagid is in Murie and Mivart's 1872 paper on the anatomy of the Lemuroidea. Therein, the authors describe the anatomy of the muscles of mastication of *Lemur catta*, and they suggest that the temporalis, the masseter, and the pterygoids are the same for *O. crassicaudatus* as for *L. catta*. They also illustrate the masticatory muscles of *O. crassicaudatus* (their Figures 3, 5, 17 and 18). Minkoff (1968) describes the masticatory muscles in two galagid specimens (presumed by Cordell (1991) to be *Otolemur garnetti*). He assigns homologies to the dissected muscle bundles using patterns of innervation. The atlas by Stevens *et al.* (1981) on the anatomy of the lesser bush baby, *Galago senegalensis*, provides a few illustrations of a superficial dissection of the muscles of mastication. This book, however, focuses on postcranial anatomy. In 1991, Cordell performed the first detailed analysis of the relationship between form and function in the masticatory muscles of galagids. Based on two specimens of *O. crassicaudatus*, four specimens of *O. garnetti*, four specimens of *Galago senegalensis* and two specimens of *Galagooides demidoff*, this thesis contains the most detailed treatment of this subject.

The literature on masticatory movements and forces in primates is reviewed in Chapter 6.

5.2.2 Anatomy and actions of the masticatory muscles of galagids

In February of 2000 and February of 2001, I examined the masticatory muscles of *O. crassicaudatus* *in situ* on a cadaver preserved in ethanol. The cadaver was in the care of

Dr. Nancy Cordell following its use in her Ph.D. study (Cordell, 1991). Its head is shown in Plate 2. I measured the apparent orientation of the fibres¹ of each masticatory muscle in two planes to estimate the true orientation of pull of each muscle. These measurements are given in Table 5-1.

muscle	apparent angle of pull		orientation ³
	x ¹	y ²	
Superficial masseter	45	40	d-l/v-m
Deep masseter	25	55	d-l/v-m
Zygomaticomandibular	20	85	d-l/v-m
Lateral pterygoid	75	-25	v-m/d-l
Medial pterygoid	15	55	d-m/v-l
Superficial temporal	15	145	d-m/v-l
Deep temporal	20	155	d-m/v-l
Zygomatic temporal	10	135	d-l/v-m
Anterior digastric	15	-170	v-l/d-m
Posterior digastric	15	-180	v-l/d-m

Table 5-1 Orientation of muscles in *Otolemur crassicaudatus*. ¹Measured as the smallest angle to the sagittal plane. ²Measured from horizontal plane. Negative value means below horizontal plane. Value greater than 90 degrees means posterior orientation. Angles are estimated from muscles *in situ* (see text). ³Listed as origin/insertion. ‘d’ signifies ‘dorso’, ‘l’ signifies ‘lateral’, ‘v’ signifies ‘ventro’ and ‘m’ signifies ‘medial’.

I also examined 70 muscles that had been isolated and removed from eight galagid specimens. These muscles were studied by Dr. Cordell for her Ph.D. dissertation. They were stored in plastic film canisters in a weak solution of formalin (5-10%). The excised muscles of one representative individual are shown in Plate 2. The masticatory musculature was divided into ten muscles per side: the superficial temporal muscle, deep temporal, zygomatic temporal, zygomaticomandibularis, superficial masseter, deep masseter, medial pterygoid, lateral pterygoid, anterior digastric and the posterior digastric muscle. The following descriptions are based partly on my study and partly on the dissertations of both E.C. Minkoff (1968) and N.N. Cordell (1991). For further detail on the anatomy of the muscles of mastication in galagids, I direct the reader’s attention to the latter.

Minkoff (1968) summarizes the evolution of the masticatory muscles in vertebrates, drawing on work by Edgeworth (1935) and others:

¹ Measured with a protractor, at a median position on the muscle surface at a point representing the median orientation of fibres, as close as possible to the bulk of the muscle mass. The true orientation of pull may be approximated more roughly by the orientation of a line drawn from the centre of the origin (on the skull) to the centre of the insertion (on the mandible) (Cordell, 1991).

The m. mylohyoideus and the anterior belly of the digastric are derived from the ventral constrictor of the mandibular arch, represented in the shark by the m. intermandibularis. The remaining muscles are all derived from the m. adductor mandibulae, which split into external, internal and posterior portions. The m. adductor mandibulae externus gave rise to the temporal, masseter, and lateral pterygoid muscles, the m. adductor mandibulae internus to the medial pterygoid, and the m. adductor mandibulae posterior to the mm. tensor tympani and tensor veli palatini (Minkoff, 1968, p. 50).

Note that Edgeworth (1935) refers to the adductor mandibulae as the ‘levator mandibulae’ and to its pars internus as ‘pars anterior’. Minkoff further divides the masseter muscle into two parts: *pars superficialis* (superficial masseter) and *pars profunda* (deep masseter). He does not subdivide the temporal, medial pterygoid or the lateral pterygoid muscles. He splits the digastric muscle into an anterior portion (see above) and a posterior portion that is derived from the interhyoideus muscle and innervated by a branch of the facial nerve.

Cordell (1991) classifies the masticatory muscles of galagids in a similar manner to that suggested by De Gueldre and De Vree (1988) for the fruit bat, *Pteropus giganteus*. She subdivides Minkoff’s ‘superficial masseter’ into the superficial masseter (laterally placed) and the deep masseter (medially placed) and refers to Minkoff’s ‘deep masseter’ as the zygomaticomandibularis. She subdivides Minkoff’s ‘temporalis’ into a superficial and a deep portion; she divides the ‘medial pterygoid’ into three bundles and the ‘lateral pterygoid’ into two. The digastric is considered two muscles by both authors.

Muscles are usually subdivided based on differences in function, fibre orientation and/or fibre length. Sometimes the division is marked by a physical landmark, such as a fascial septum or an aponeurosis. One could conceivably divide each muscle down to the level of the individual fibres, and then give each fibre a separate name; each fibre has a slightly different orientation, separates evenly and has a different length. At some point, however, one must appeal to expedience.

For the purposes of this thesis, I will adhere to Cordell’s classification for all muscles but the pterygoids. The pterygoid musculature is here considered two muscles: the medial pterygoid and the lateral pterygoid. Cordell makes an excellent case for subdividing the medial and lateral pterygoids based on anatomical features and functional considerations. Regardless, each of these muscles is very small and difficult to measure in galagos, so my choice not to subdivide them is made for the sake of convenience. Also, further subdivision is unlikely to affect my results.

5.3 Brief description of the individual masticatory muscles of galagids

For the following descriptions, information on muscle insertions, origins and actions are from Minkoff (1968), Cordell (1991) and from personal observation.

5.3.1 *The temporal muscle group*

The temporal muscle group is composed of a large fan-like sheet that covers the lateral aspect of the skull in galagids. It is the largest of the galagid masticatory muscle groups. It is composed of a superficial, a deep and a zygomatic portion in galagos.

5.3.1.1 Superficial temporal

The superficial temporal muscle originates from the temporal fossa, including origins from the frontal, parietal and squamosal bones. The origin of this muscle lies as far dorsal as the superior temporal line and as far posterior as the nuchal crest. Some fibres arise from the postero-dorsal aspect of the zygomatic arch and others arise from the superficial surface of the deep temporal muscle. The superficial temporal inserts by two heads onto the antero-lateral aspect of the coronoid process of the mandible and onto the antero-medial aspect of the coronoid process. The anterior fibres of the superficial temporal are oriented in a more near-vertical plane and the posterior fibres are oriented more horizontally. Fibres converge and course medially toward the point of insertion. Acting bilaterally, the superficial temporal muscles elevate and slightly retract the mandible². Acting unilaterally, the superficial temporal swings the mandible slightly contralaterally (i.e., the right superficial temporal swings the mandible slightly to the left). Table 5-1 shows the apparent angles for the average orientation of this muscles' fibres (as well as those for all other muscles).

5.3.1.2 Deep temporal

The deep portion of the temporal muscle is very similar to the superficial portion. It is also a fan-shaped sheet. It also originates from the temporal fossa and it is mostly overlain by the superficial temporal. It inserts onto the medial aspect of the coronoid

² When it is in a protracted position, having been thrust forward by the action of other muscles, the mandible is returned to its resting position by the action of the superficial temporals.

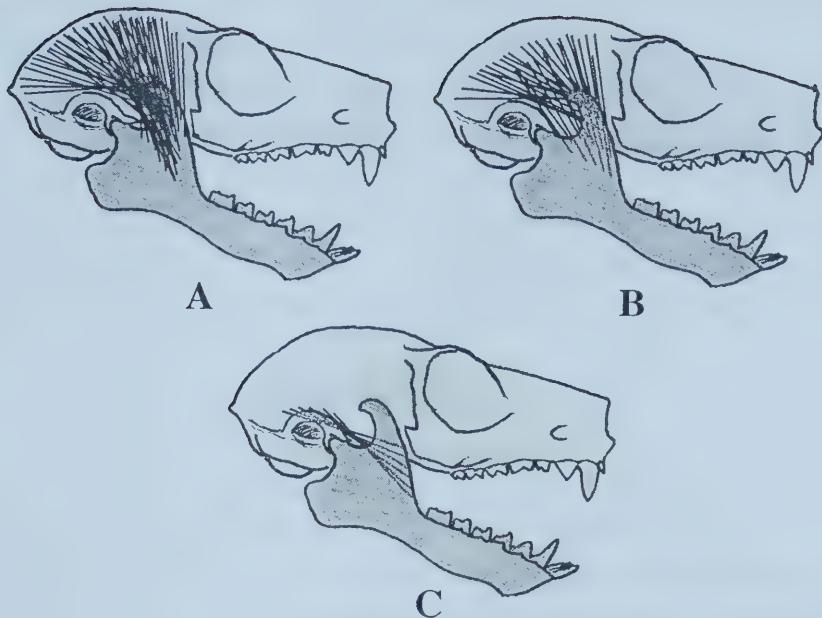


Figure 5-1 Approximate positions of temporal muscles in *Otolemur crassicaudatus*. Lateral views. Black bars approximate muscle fibres. Solid bars are in full view. Hazy bars are behind bones. The zygomatic arch has been cut away to better view the muscle fibres. A, superficial temporal; B, deep temporal; C, zygomatic temporal.

process, from the anterior border to the posterior border. The anterior fibres of the deep temporal are oriented more vertically than the posterior ones, though all fibres course medially toward the insertion. The deep temporal can be distinguished from the superficial temporal based on the much more horizontal orientation of its fibres.

The action of this muscle is very similar to that of the superficial temporal, though the deep temporal retracts the mandible more markedly due to the more horizontal orientation of its fibres.

5.3.1.3 Zygomatic temporal

The zygomatic portion of the temporal is much smaller than the other two portions and it is crescentic in shape. It originates from the medial side of the zygomatic arch, at the junction of the post-orbital bar and the zygomatic arch. Fibres course medially in a horizontal direction and arch ventrally in a vertical direction to insert on the lateral aspect of

the anterior border of the coronoid process. Some of the deeper fibres of the zygomatic temporal interdigitate with those of the superficial temporal; some superficial fibres interdigitate with those of the zygomaticomandibular.

The zygomatic temporal elevates and retracts the mandible when both sides are used together (bilateral action). When it acts unilaterally, it swings the mandible in the ipsilateral direction (i.e., the right zygomatic temporal swings the mandible to the right).

The design for my mastication machine considers the zygomatic temporal and the superficial temporal to be one muscle: the superficial temporal. The forces (magnitudes and orientations) of these muscles are summed and represented by a single cable on each side.

5.3.2 *The masseter muscle group*

The masseter group is composed of three rhomboidal, sheet-like layers from the superficial masseter (lateral-most) to the zygomaticomandibular (medial-most). It is the next largest group, after the temporals. Though all fibres are oriented antero-dorso-lateral to postero-ventro-medial, the deepest fibres of this muscle group are the most vertical and the most superficial fibres are the most horizontally oriented.

5.3.2.1 Superficial masseter

The superficial masseter is by far the largest muscle of this group. It is a bulbous mass that originates from the ventral margin and the ventral half of the lateral surface of the zygomatic arch, extending from the zygomatic process of the squamosal posteriorly to the zygomatic process of the maxilla anteriorly. The fibres of this muscle course posteriorly, ventrally and medially; the anterior fibres are oriented more horizontally than the posterior ones. This muscle inserts onto the angular process of the mandible, in a trough on its lateral surface and on the ventral and posterior borders of the horizontal ramus of the mandible, extending dorsally onto the posterior surface of the lateral process of the mandibular condyle.

Acting bilaterally, the superficial masseter elevates and protracts the mandible. Acting unilaterally, it swings the mandible ipsilaterally (i.e., the right masseter swings the mandible to the right).

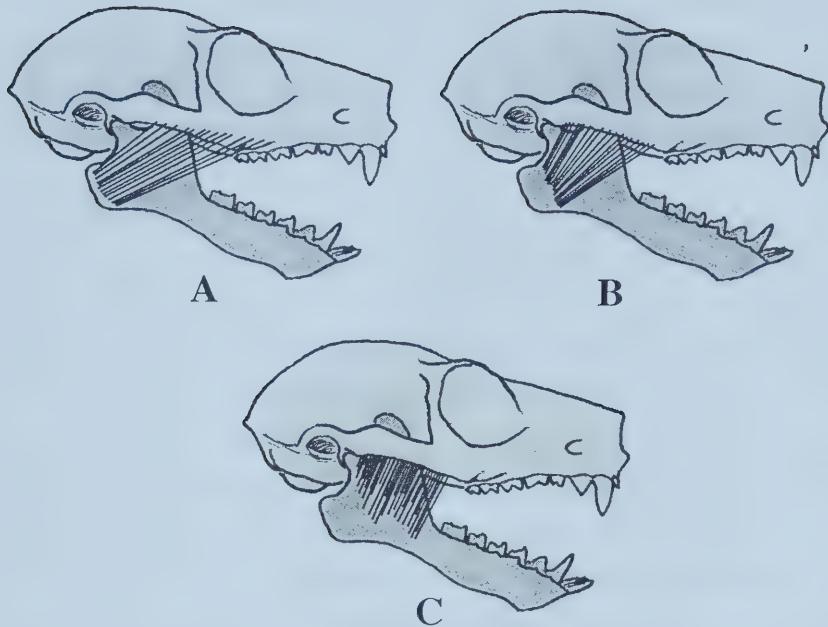


Figure 5-2 Approximate positions of masseter muscles in *Otolemur crassicaudatus*.

Lateral views. Black bars approximate muscle fibres. Solid bars are in full view. Hazy bars are behind bones. A, superficial masseter; B, deep masseter; C, zygomaticomandibular.

5.3.2.2 Deep masseter

The deep portion of the masseter is a thin sheet that resembles the superficial masseter with respect to the orientation of the fibres as well as to the origin and insertion points.

This muscle originates on the ventral surface of the zygomatic arch, from the jugal posteriorly and from the zygomatic process of the maxilla anteriorly. Fibres course ventrally, posteriorly and slightly medially, to insert on the lateral surface of the mandibular ramus, antero-dorsal to the insertion of the superficial masseter.

The action of this muscle is similar to that of the superficial masseter, although the deep masseter possesses more vertically oriented fibres and therefore acts less to protract the mandible and more to elevate it. It is also less capable of swinging the mandible laterally.

5.3.2.3 Zygomaticomandibular

The zygomaticomandibular is morphologically similar to the deep masseter. This is the muscle identified by Minkoff (1968) as the deep masseter. It is a thin sheet that lies medial to the deep masseter inside the masseteric fossa of the mandible. Its anterior portion interdigitates with the deep masseter, while its deep portion interdigitates with the superficial temporal and the zygomatic temporal.

The zygomaticomandibular originates on the medial surface of the zygomatic arch, alongside the origin for the deep masseter. Its fibres course ventrally, slightly posteriorly and slightly medially, although most of the fibres are nearly vertical. This muscle inserts into the masseteric fossa, dorsal and anterior to the insertion for the deep masseter.

The zygomaticomandibular acts in a similar fashion to the deep masseter, though it acts even more to elevate and less to protract the mandible. I have some doubt as to whether or not this muscle should be considered distinct from the deep masseter. It is rather difficult to separate the two in a dissection. It is possible that both the zygomaticomandibular and the zygomatic portion of the temporal are simply ‘zones of gradation’ between the masseter group and the temporal group.

For simplicity, I have combined the zygomaticomandibular with the deep masseter in the design of my machine. I summed the magnitudes and orientations of the forces they produce and I used one cable (per side) to simulate both. The combined muscle is heretofore referred to as the deep masseter.

5.3.3 *The pterygoid muscle group*

Though some might separate this muscle group into several components, it is expedient to consider only two: the medial pterygoid muscle and the lateral pterygoid muscle. Both muscles are relatively small and inaccessible in primates; perhaps they are poorly studied for this reason. It is difficult to insert an electrode in either muscle (especially the lateral pterygoid) for electromyographic analysis, and it is difficult to see these muscles in dissection without removing a great deal of tissue. Furthermore, the fibres of both muscles diverge considerably at the origin, making function difficult to discern. It is thought, however, that both muscles act to move the mandible in the medio-lateral plane.

Separation of the medial pterygoid from the lateral pterygoid is based on homology. The lateral pterygoid (along with the masseters and temporals) is derived from the primitive adductor mandibulae externus, whereas the medial pterygoid is derived from the adductor mandibulae internus (Minkoff, 1968, see above).

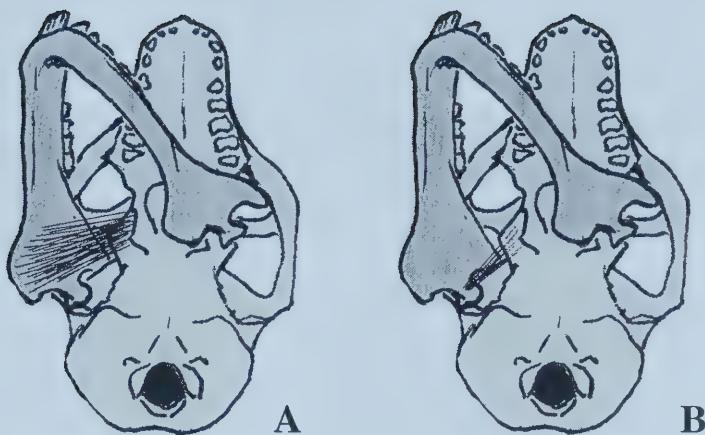


Figure 5-3 Approximate positions of pterygoid muscles in *Otolemur crassicaudatus*.

Basal views. Black bars approximate muscle fibres. Solid bars are in full view. Hazy bars are behind bones. A, medial pterygoid; B, lateral pterygoid.

5.3.3.1 Medial pterygoid

The medial pterygoid muscle is the larger of the two pterygoid muscles. It originates from three locations: 1. the lateral surface of the medial pterygoid hamulus and the pterygoid fossa, 2. the medial surface of the lateral pterygoid plate and 3. the medial surface of the orbit. The bundles originating from these separate locations are considered different muscle heads by Cordell (1991). They are the medial, intermediate and orbital heads respectively. Fibres from all three heads course posteriorly, ventrally and laterally and they converge upon the point of insertion. The medial pterygoid muscle inserts on the medial surface of the dentary angle.

The medial pterygoid muscles elevate and protract the mandible when they act in concert. Acting unilaterally, this muscle swings the mandible contralaterally (i.e., the right medial pterygoid muscle swings the mandible to the left). The medial pterygoid muscle is thought to have a primary role in the medial excursion of the mandible during the grinding phase of mastication. Therefore, one would expect this muscle to be larger in the earliest primates than in their primitive eutherian ancestors (Jablonski, 1986).

I simulated the medial pterygoid using one cable only (per side) in the design for the mastication machine.

5.3.3.2 Lateral pterygoid

This muscle is perhaps the most poorly understood of all the muscles of mastication. It is often divided into two heads that may or may not have different functions (see Grant, 1973 and McNamara, 1973). Confusion also arises as the orbital head of the medial pterygoid muscle has been misidentified in galagos as the lateral pterygoid muscle (e.g., Murie and Mivart, 1872).

The lateral pterygoid lies dorsal and lateral to the medial pterygoid. Its upper head originates from the greater wing of the sphenoid bone and the ventral surface of the squamosal bone anterior to the glenoid fossa. The lower head originates from the lateral surface of the lateral pterygoid plate. The fibres of the upper head course posteriorly, laterally and ventrally, whereas those of the lower head course posteriorly, laterally and *dorsally*. Hence the confusion as to function when both heads are considered together. The fibres of both heads converge and insert onto the mandible at a point slightly ventral, medial and anterior to the mandibular condyle.

As the upper head of the lateral pterygoid muscle acts bilaterally, but independently of the lower head, it protracts and elevates the mandible. As the lower head acts bilaterally, but independently of the upper head, it protracts and *depresses* the mandible. It is thought that the lateral pterygoid heads may act together during mastication to stabilize the temporomandibular joint. Acting unilaterally, either head of this muscle causes the mandible to swing contralaterally (i.e., the right lateral pterygoid muscle swings the mandible to the left).

I had some difficulty deciding how best to simulate this muscle experimentally. Eventually, I decided to simulate only the lower head. To simulate the upper head, it would have been necessary to make considerable modifications to the skull I used in the machine. Such modifications would have weakened the skull, increasing its vulnerability to mechanical failure during chewing tests. The upper head of the lateral pterygoid muscle exerts only a small amount of force and it performs the same action as a number of stronger muscles (e.g., medial pterygoid and to a lesser degree, the masseter group). For these reasons, it did not seem necessary to simulate it.

Therefore, the cable representing the lateral pterygoid in my machine approximates the orientation and action of the lower head only. It depresses and protracts the mandible slightly. I have, however, added the strength of the upper head to that of the lower head for this single cable (one per side). This approximates the condition of the lateral pterygoid in some other mammals, such as the little brown bat (Kallen and Gans, 1972), wherein this muscle is a single functional unit that protracts and depresses the mandible.

5.3.4 The digastric muscle group

This muscle group consists of the principle jaw abductors in primates: the anterior digastric and the posterior digastric. These are long, thin muscle bands that course from the base of the skull to the medial border of the mandible near the symphysis. The anterior portion is simply the anterior continuation of the posterior portion and the two are joined by a short tendon posterior and medial to the mandibular angle.

The subdivision of the digastric muscle is justified because the anterior portion is derived from the primitive intermandibularis muscle, whereas the posterior portion is derived from the primitive interhyoideus (Minkoff, 1968, see above).

5.3.4.1 Anterior digastric

This lanceolate muscle originates from the digastric tendon (the junction with the posterior digastric). Fibres course anteriorly, medially and very slightly dorsally toward the insertion on the ventro-medial surface of the horizontal ramus of the mandible. The insertion extends posteriorly from near the mandibular symphysis (usually below the p4) to a point level with the anterior border of the masseteric fossa (Cordell, 1991).

This muscle depresses and retracts the mandible.

5.3.4.2 Posterior digastric

This muscle is shaped very much like the anterior digastric. It originates from “the ventral surface of the tympanic bulla ventral, medial and caudal to the external auditory meatus” (Cordell, 1991, p.156). The fibres course anteriorly, medially and slightly ventrally. The digastric tendon thins and runs deeply inside the posterior digastric muscle. The fibres of the posterior digastric muscle converge and insert on this tendon.

This muscle acts on the anterior digastric to depress and retract the mandible.

The mastication machine simulates a single digastric muscle (per side). Values of magnitude and orientation of force in these two muscles were averaged to generate the specifications for the paired digastric muscle cable.

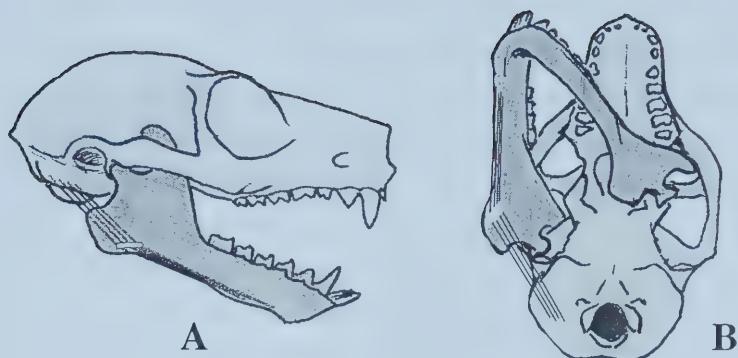


Figure 5-4 Approximate positions of digastric muscles in *Otolemur crassicaudatus*.

Black bars approximate muscle fibres. Solid bars are in full view. Hazy bars are behind bones. Anterior digastric fibres are anterior; posterior digastric fibres are posterior. A white bar represents the point of fusion between these muscles. A, lateral view; B, basal view.

5.4 Relative forces of the masticatory muscles of galagids

5.4.1 EMG and PCS

Electromyography (or EMG) is the most commonly used method for measuring the force of a muscle during normal activity. This method consists of inserting an electrode into a muscle in a living subject and measuring its electric action potential while the subject performs a designated activity. The electrical potential is recorded and interpreted to estimate the forces produced by the muscle during that activity. This method was first applied to the masticatory muscles by Moyers (1949). Since, it has been used extensively to estimate forces produced by the masticatory muscles during chewing for a number of living mammals (e.g., Kallen and Gans, 1972; Vitti and Basmajian, 1977; Byrd and Garthwaite, 1981; Hylander *et al.*, 1987; De Gueldre and De Vree, 1988). Unfortunately, electromyography has not been performed on the masticatory muscles of galagids.

One disadvantage of EMG is that it is necessary to have a living, co-operative subject. This is easy to achieve with humans, but many primates, such as galagids, are relatively rare in captivity. Galagos in particular are sometimes unwilling to perform in experimental situations (Hylander, 1979). In such situations, or when the only available specimens are cadavers, the physiological cross-section of a muscle gives a good approximation of the force it normally exerts.

The physiological³ cross-sectional area (or PCS) of a muscle is probably the best estimator of relative muscle force when the PCS for several muscles is compared (Weijs and Hillen, 1985; Anton, 1999). PCS has interested muscle physiologists for a long time. In 1846, Weber (see Weijs and Hillen, 1985) proposed that it can be measured by dividing the weight of a muscle by the mean length of its fibres. It is thus calculated the same way one calculates the surface area of the flat top of a cylinder. The mean length of muscle fibres within the muscle represents the height of the cylinder.

The physiological cross-sectional area of the masticatory muscles has been measured for a few mammals, including humans (e.g., Weijs and Hillen, 1985), rats (Rayne and Crawford, 1972), fruit bats (De Gueldre and De Vree, 1990) and macaques (e.g., Anton, 1999). Until now, the PCS of galagid masticatory muscles had not been measured.

5.4.2 Materials and methods

In February 2000 and again in February 2001, I measured the weights and fibre lengths of several galagid masticatory muscles. The muscles measured were from eight specimens (i.e., cadavers) that represent four species of galagids. Two of the measured specimens were from the Oregon Regional Primate Center (ORPC), three were from the Arizona State University (ASU), two were from the North Carolina Zoological Park (NCZP) and one was from the collection of D. E. Haines (Haines).

I measured the muscles from both sides of two specimens of *Otolemur crassicaudatus* (ORPC female #1 and ORPC female #2), from only the left side of two specimens of *O. garnetti* (ASU male #1 and Haines male A), from only the left side of two specimens of *Galago senegalensis braccatus* (ASU female E and ASU female Jf), from the left side of one specimen of *Galago demidoff* (NCZP female 507) and from the right side of another specimen of *G. demidoff* (NCZP female 510). All muscles studied were from dentally adult galagos (Cordell, 1991). All but one specimen were complete with respect to the masticatory musculature: the brain of the Haines specimen had been removed and much of the temporalis musculature was lost. Therefore, this specimen is omitted from the final analysis.

For each muscle, I followed the procedure detailed in Rayne and Crawford (1972) for determining physiological cross-sectional area. Each muscle was patted dry with a paper towel and immersed in a 10% solution of sulfuric acid. The muscle was then cooked

³ This is different from the actual cross-sectional area in that it is an estimate - not a measurement - of area.

in an oven at about 60°C for one to four hours, depending on the size of the muscle. This process dissolves most of the connective tissue surrounding the muscle fibres, not only making it easier to measure the fibre length, but also eliminating the connective tissue from muscle weight measurements.

Once each muscle was cooked, it was patted and squeezed dry with a paper towel and weighed using an electronic scale. Despite the patting, this value is essentially a ‘wet weight’ value. The weight of each muscle is given in Table 5-3 (weight = mean fiber length x index of PCS).

With the aid of a dissecting microscope, forceps and dissecting pins, fasciculi of 10-20 fibres each were separated from the rest of the muscle mass. For each muscle, the lengths of 30 such fasciculi were measured (to the tenth of a millimetre). The mean fibre lengths are given in Table 5-2.

Each muscle’s weight was divided by its mean fibre length to obtain its physiological cross-sectional area. The PCS for each galagid specimen is given in Table 5-4.

5.4.3 *Results*

In galagos, the temporal muscles have the largest area of physiological cross-section; therefore, they exert the most force during their normal activity (mastication). The masseter muscle group is about half as strong as the temporal muscle group. The pterygoid group is about a quarter as strong as the temporal group and the digastric group is about a tenth as strong (see Table 5-4).

The deep temporal is the strongest individual muscle, followed by the superficial masseter then the superficial temporal. The medial pterygoide, the deep masseter, the zygomatic temporal and then the zygomaticomandibular follow. On average, the weakest muscle is the anterior digastric. The second weakest muscle is the posterior digastric, closely followed by the lateral pterygoid.

The size (i.e., mass) of the masticatory muscles follows the same pattern as the PCS, with one exception. The posterior digastric is actually larger than the lateral pterygoid, despite the greater strength of the latter. This is due to the great length of most muscle fibres in the posterior digastric. This muscle acts principally to depress the mandible. Such an action requires little strength because it is assisted by gravity (unless the primate in question is an upside-down suspensor). Speed is an asset to all masticatory muscles because a higher rate of mastication favours a high food-intake. The digastric muscles are not constrained by the need to exert very strong forces because they do not have to cause

food to break; therefore, they can be optimized for greater speed. Moreover, the posterior digastric muscle acts (given the origin and insertion) and stretches over a long distance to allow for a wide gape. A wide gape is adaptive for primates because they often either ingest large items of food or prepare them with the incisors. These factors favour long fibres in the posterior digastric muscle.

On average, the fibres of the posterior digastric are the longest and those of the medial pterygoid muscle are the shortest. Fibres of the temporal musculature are generally long while those of the masseter are medium in length and those of the pterygoids are short. This suggests that the fibres of the temporals favour fast action, those of the pterygoids are relatively strong, and those of the masseter group are intermediate. There is a great deal of variation in fibre length in both the temporal group and in the superficial masseter, suggesting they can act either rapidly or strongly, whereas the fibres in the other masticatory muscles are relatively uniform.

5.4.3.1 *Otolemur crassicaudatus*

The pattern of PCS in the masticatory muscles of *O. crassicaudatus* is similar to that described above for galagids in general. However, the deep temporal is only slightly stronger than the superficial masseter in this species. Also, the zygomatic temporal is stronger than the deep masseter. Muscle weights for *O. crassicaudatus* follow the same pattern.

This species is particularly important because I used it to model the forces generated by the mastication machine. The machine forces are given in Chapter 6 (Table 6-1). Despite the relative strengths of the superficial and deep temporal, shown in Table 5-4, I have modeled the superficial temporal as a stronger muscle. This is due to the fact that I designed the machine after having measured the muscles from only one side of a single individual (ORPC female #1, from the left side). Regardless of which is the strongest, the difference in strength in these two muscles is minor.

The lengths of the masticatory muscle fibres in *O. crassicaudatus* follow the same pattern as that described for galagids in general.

5.4.3.2 *Otolemur garnetti*

It is difficult to assess relative muscle strength in *O. garnetti* from this study because a significant part of the musculature was missing in one of the two available

<i>Otolemur crassicaudatus</i>	Deep temp.	Sup. mass.	Sup. temp.	Med. pter.	Deep mass.	Zyg. temp.	Zygm.	Lat. pter.	Post. dig.	Ant. dig.
ORPC 1F left	7.46	7.12	7.70	6.72	5.79	8.62	6.55	5.64	9.05	5.45
ORPC 1F right	6.80	6.43	8.10	5.44	6.96	7.43	7.26	5.77	9.82	7.46
ORPC 2F left	6.91	7.30	7.12	4.43	7.18	6.73	5.20	7.95	9.21	5.90
ORPC 2F right	6.46	5.90	8.56	4.68	5.27	8.68	5.33	4.78	5.54	5.77
MEAN	6.91	6.69	7.87	5.32	6.30	7.87	6.08	6.04	8.41	6.15
<i>Otolemur garnetti</i>										
ASU 1M left	7.38	8.54	8.78	5.72	8.83	8.99	6.96	6.67	10.33	7.87
Haines AM left	N/A	8.50	7.08	4.50	7.97	12.79	N/A	5.89	6.66	5.66
MEAN	3.69	8.52	7.93	5.11	8.40	10.89	3.48	6.28	8.49	6.76
<i>Galago senegalensis braccatus</i>										
ASU EF left	6.10	6.73	7.11	5.43	4.55	7.16	4.04	6.03	6.54	3.96
ASU JfF left	6.09	4.68	5.80	4.14	5.18	5.31	4.41	4.46	6.12	3.89
MEAN	6.09	5.70	6.46	4.79	4.86	6.24	4.23	5.25	6.33	3.92
<i>Galagooides demidoff</i>										
NCZP 510F right	3.15	4.12	3.07	3.26	3.71	3.98	3.41	2.80	4.71	4.08
NCZP 507F left	4.05	4.00	4.40	2.77	2.93	4.36	3.84	3.25	5.29	3.33
MEAN	3.60	4.06	3.74	3.01	3.32	4.17	3.62	3.02	5.00	3.70
GRAND MEAN	5.99	6.25	6.71	4.71	5.83	6.82	5.22	5.24	7.52	5.41

Table 5-2 Mean fibre length of masticatory muscles in galagos. Fibre lengths are given in millimetres. Abbreviations for specimens are as follows: ORPC, Oregon Regional Primate Center; ASU, Arizona State University; Haines, from the collection of Duane Haines; NCZP, North Carolina Zoological Park. ‘F’ stands for a female individual and ‘M’ stands for a male. ‘L.’ stands for muscle from the left side of the body and ‘R.’ stands for muscles from the right. The grand mean does not include values for the Haines specimen.

specimens. The following observations concern the single complete specimen, though Table 5-2, 5-3 and 5-4 list the values for the incomplete Haines specimen as well.

With respect to both PCS and muscle size, *O. garnetti*’s masticatory muscles follow the pattern described for galagids in general. This is not simply due to the large size of the muscles in this species ‘swamping’ the values for smaller species in the calculated mean for galagids. The same pattern emerged when I calculated the proportions of muscle strengths within a species and then compared different species with respect to those proportions.

The lengths of the fibres in *O. garnetti* are similar to the mean lengths for the galagids in general.

<i>Otolemur crassicaudatus</i>	Deep temp.	Sup. mass.	Sup. temp.	Med. pter.	Deep mass.	Zyg. temp.	Zygm.	Lat. pter.	Post. dig.	Ant. dig.
ORPC 1F left	2.146	1.842	1.937	0.815	0.404	0.525	0.238	0.209	0.288	0.102
ORPC 1F right	1.535	1.071	1.299	0.407	0.177	0.282	0.168	0.101	0.213	0.092
ORPC 2F left	1.846	1.828	1.363	0.591	0.196	0.423	0.280	0.243	0.184	0.066
ORPC 2F right	1.624	1.559	1.380	0.518	0.211	0.309	0.188	0.151	0.126	0.080
MEAN	1.788	1.575	1.495	0.583	0.247	0.385	0.219	0.176	0.203	0.085
<i>Otolemur garnetti</i>										
ASU 1M left	2.211	2.124	1.982	0.633	0.590	0.367	0.235	0.150	0.232	0.127
Haines AM left	N/A	1.643	0.721	0.397	0.832	0.241	N/A	0.068	0.161	0.109
MEAN	1.106	1.884	1.352	0.515	0.711	0.304	0.118	0.109	0.197	0.118
<i>Galago senegalensis braccatus</i>										
ASU EF left	0.376	0.252	0.210	0.113	0.037	0.041	0.039	0.037	0.039	0.025
ASU JFF left	0.378	0.244	0.221	0.120	0.045	0.052	0.056	0.028	0.030	0.026
MEAN	0.377	0.248	0.216	0.117	0.041	0.047	0.048	0.033	0.035	0.026
<i>Galago demidoff</i>										
NCZP 510F right	0.051	0.041	0.026	0.021	0.007	0.010	0.008	0.005	0.009	0.005
NCZP 507F left	0.064	0.051	0.024	0.023	0.009	0.011	0.010	0.008	0.010	0.004
MEAN	0.058	0.046	0.025	0.022	0.008	0.011	0.009	0.007	0.010	0.005
GRAND MEAN	1.108	0.998	0.929	0.339	0.222	0.202	0.128	0.091	0.120	0.061

Table 5-3 Weight of masticatory muscles of galagos. Weight values are given in grams. Abbreviations for specimens are as follows: ORPC, Oregon Regional Primate Center; ASU, Arizona State University; Haines, from the collection of Duane Haines; NCZP, North Carolina Zoological Park. ‘F’ stands for a female individual and ‘M’ stands for a male. ‘L.’ stands for muscle from the left side of the body and ‘R.’ stands for muscles from the right. The grand mean does not include values for the Haines specimen.

5.4.3.3 *Galago senegalensis braccatus*

Individuals of this species are much smaller (~213g) than those of *O. crassicaudatus* (~1159g) and *O. garnetti* (~764g) (Fleagle, 1999), though patterns of PCS are similar in all three species. However, the masticatory muscles of *G. senegalensis braccatus* are weaker overall than those of the larger species. As well, when muscle strength of each muscle is expressed as a multiple of the strength of the weakest muscle (anterior digastric), the masticatory muscles of *G. senegalensis braccatus* appear to be weaker. The relative strengths of these muscles plot similarly to those of galagids in general, with a few exceptions. The zygomaticomandibular is stronger than the deep masseter and the zygomatic temporal; the anterior digastric is stronger than the lateral

<i>Otolemur crassicaudatus</i>	Deep temp.	Sup. mass.	Sup. temp.	Med. pter.	Deep mass.	Zyg. temp.	Zygm.	Lat. pter.	Post. dig.	Ant. dig.
ORPC 1F left	2.9E-1	2.6E-1	2.5E-1	1.2E-1	7.0E-2	6.1E-2	3.6E-2	3.7E-2	3.2E-2	1.9E-2
ORPC 1F right	2.3E-1	1.7E-1	1.6E-1	7.5E-2	2.5E-2	3.8E-2	2.3E-2	1.7E-2	2.2E-2	1.2E-2
ORPC 2F left	2.7E-1	2.5E-1	1.9E-1	1.3E-1	2.7E-2	6.3E-2	5.4E-2	3.1E-2	2.0E-2	1.1E-2
ORPC 2F right	2.5E-1	2.6E-1	1.6E-1	1.1E-1	4.0E-2	3.6E-2	3.5E-2	3.2E-2	2.3E-2	1.4E-2
MEAN	2.6E-1	2.3E-1	1.9E-1	1.1E-1	4.1E-2	4.9E-2	3.7E-2	2.9E-2	2.4E-2	1.4E-2
<i>Otolemur garnetti</i>										
ASU 1M left	3.0E-1	2.5E-1	2.3E-1	1.1E-1	6.7E-2	4.1E-2	3.4E-2	2.3E-2	2.2E-2	1.6E-2
Haines AM left	N/A	1.9E-1	1.0E-1	8.8E-2	1.0E-1	1.9E-2	N/A	1.2E-2	2.4E-2	1.9E-2
MEAN	1.5E-1	2.2E-1	1.6E-1	9.9E-2	8.6E-2	3.0E-2	1.7E-2	1.7E-2	2.3E-2	1.8E-2
<i>Galago senegalensis braccatus</i>										
ASU EF left	6.2E-2	3.7E-2	3.0E-2	2.1E-2	8.1E-3	5.7E-3	9.6E-3	6.1E-3	6.0E-3	6.3E-3
ASU JfF left	6.2E-2	5.2E-2	3.8E-2	2.9E-2	8.7E-3	9.8E-3	1.3E-2	6.3E-3	4.9E-3	6.7E-3
MEAN	6.2E-2	4.5E-2	3.4E-2	2.5E-2	8.4E-3	7.8E-3	1.1E-2	6.2E-3	5.4E-3	6.5E-3
<i>Galagooides demidoff</i>										
NCZP 510F right	1.6E-2	1.0E-2	8.5E-3	6.4E-3	1.9E-3	2.5E-3	2.3E-3	1.8E-3	1.9E-3	1.2E-3
NCZP 507F left	1.6E-2	1.3E-2	5.5E-3	8.3E-3	3.1E-3	2.5E-3	2.6E-3	2.5E-3	1.9E-3	1.2E-3
MEAN	1.6E-2	1.1E-2	7.0E-3	7.4E-3	2.5E-3	2.5E-3	2.5E-3	2.1E-3	1.9E-3	1.2E-3
GRAND MEAN	1.6E-1	1.3E-1	1.1E-1	6.3E-2	3.0E-2	2.5E-2	2.1E-2	1.5E-2	1.3E-2	9.5E-3

Table 5-4 PCS index of masticatory muscles in galagos. Values are given in grams / millimetres and are expressed in scientific notation (2.9E-1 = 0.29). Abbreviations for specimens are as follows: ORPC, Oregon Regional Primate Center; ASU, Arizona State University; Haines, from the collection of Duane Haines; NCZP, North Carolina Zoological Park. ‘F’ stands for a female individual and ‘M’ stands for a male. ‘L.’ stands for muscle from the left side of the body and ‘R.’ stands for muscles from the right. The grand mean does not include values for the Haines specimen.

pterygoid and the posterior digastric. Furthermore, the anterior digastric (the weakest muscle of mastication in the three other species) is stronger than the posterior digastric and the lateral pterygoid.

Muscle weight is distributed similarly to that in galagids in general. However, the zygomaticomandibular is heavier than the deep masseter and the zygomatic temporal; the zygomatic temporal is heavier than the deep masseter.

Relative fibre length is average in this species, though the digastric muscles have short fibres, relative to those in other galagid species.

5.4.3.4 *Galago demidoff*

Masticatory muscles in this species are particularly weak and light (both absolutely and relatively). Individuals of *Galago demidoff* are by far the smallest of the galagids examined (~62g) (Fleagle, 1999). Muscle weight follows the galagid pattern. PCS mostly follows this pattern too, though the medial pterygoid appears exceptionally strong in this species. Relative fibre lengths follow very closely the general pattern for galagids.

5.4.4 Implications for galagids in general

For the following sections, I refer to diet alone to explain variation in masticatory muscle strength. Uncertainty about the phylogenetic relationships among bushbabies (Rasmussen and Nekaris, 1998) prevents me from ruling out phylogenetic effects on masticatory muscle strength.

Figure 5-5 shows the relative strengths of the masticatory muscles in the four species tested. The value for each muscle is expressed as a multiple of the PCS index of the anterior digastric muscle (usually the weakest).

The strength of the masticatory muscles⁴ in each species (y-axis) is plotted against the mean strength for all four species (x-axis) in Figure 5-6. Points falling above the trendline for a given species represent muscles that are particularly strong compared to the galagid mean.

In the wild, galagids feed on a variety of items. Their main food sources are fruits, gums (especially those of acacia trees), and insects. Some predation on small vertebrates has been reported, though the evidence is questionable (see Charles-Dominique and Bearder, 1979). As only galagids were studied, it is difficult to say anything significant about the muscles of mastication of galagids relative to those of other primates. However, PCS has been measured for several monkeys, orangutans, humans, the fruit bat and the rat. In the case of the fruit bat, PCS was measured for the specific muscles studied here. In all other cases, the masticatory complex was divided into the masseter, temporal, medial pterygoid and lateral pterygoid only; in these studies, the digastric muscles were not measured.

⁴ Expressed as a multiple of the strength of the anterior digastric.

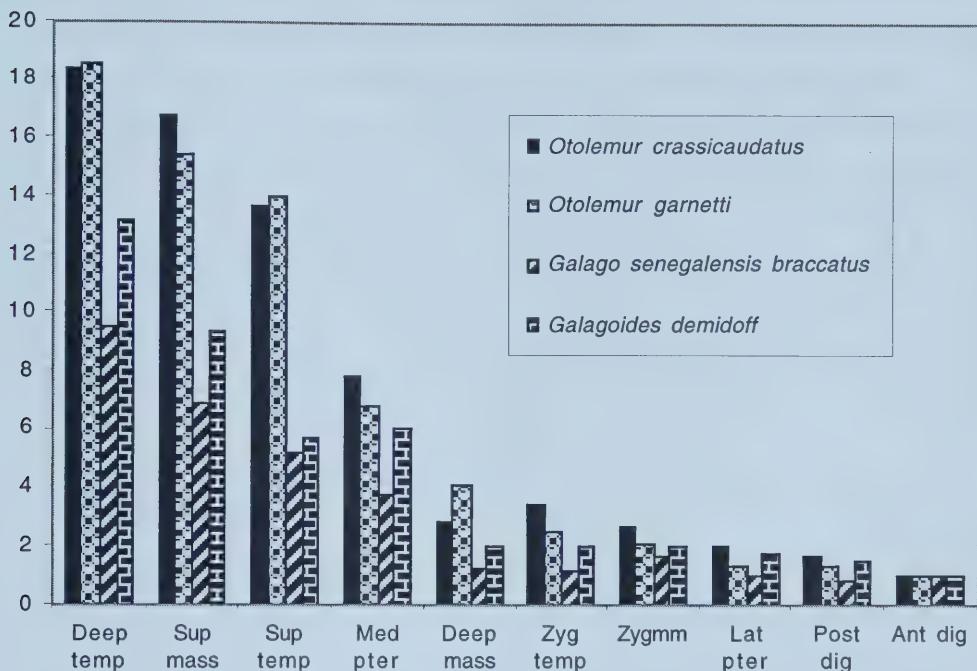


Figure 5-5 Relative muscle strength in galagids. y-axis values for a given species are multiples of the PCS index of the anterior digastric in that species (hence the ‘ant dig’ = 1 for all species). Thus, in *O. crassicaudatus* the deep temporal is approximately 18.5 times stronger than the anterior digastric.

De Gueldre and De Vree (1990) measured the PCS in the fruit bat, *Pteropus giganteus*. They divided the masticatory muscle complex in a manner similar to that adopted here (from Cordell, 1991). However, their ‘zygomaticomandibularis’ is equivalent to the ‘deep masseter’ + the ‘zygomaticomandibularis’ of Cordell (1991). The ‘superficial masseter’ of Cordell (1991) is equivalent to the ‘superficial masseter’ + the ‘deep masseter’ of De Gueldre and De Vree (1990). This difference artificially deflates the PCS value they give for the superficial masseter of the fruit bat, and concomitantly inflates the value they give for the zygomaticomandibular.

Despite these differences in muscle designation, the pattern of relative strength in the masticatory complex of *Pteropus giganteus* is very similar to that observed here for galagids. There is one noteworthy exception: the digastric muscles are very strong in the fruit bat. The anterior digastric is stronger than the lateral pterygoid and the posterior digastric is stronger than either the zygomaticomandibular or the zygomatic temporal. One would expect the digastric muscles to be stronger in a mammal that spends much of its time

chewing in an upside-down posture because these muscles must depress the mandible against the force of gravity. This appears to be the case in *Pteropus giganteus*, a mammal that often eats while hanging upside-down (Nowak and Paradiso, 1983, p. 175).

Schumacher (1961) measured the PCS in the masseter, temporal, medial pterygoid and the lateral pterygoid in the following primates: *Cebus "variegata"*, *Cebus apella*, *Macaca mulatta*, *Macaca sinica*, *Papio sp.*, *Mandrillus sp.*, *Colobus sp.* and *Homo sapiens*. Weijs and Hillen (1985) also measured PCS in humans, and Rayne and Crawford (1972) measured PCS in the same muscles in the "Lister rat". For all primates measured (including galagids), the temporal is the strongest muscle, followed by the masseter, the medial pterygoid and the lateral pterygoid. Only in the rat is the masseter stronger than

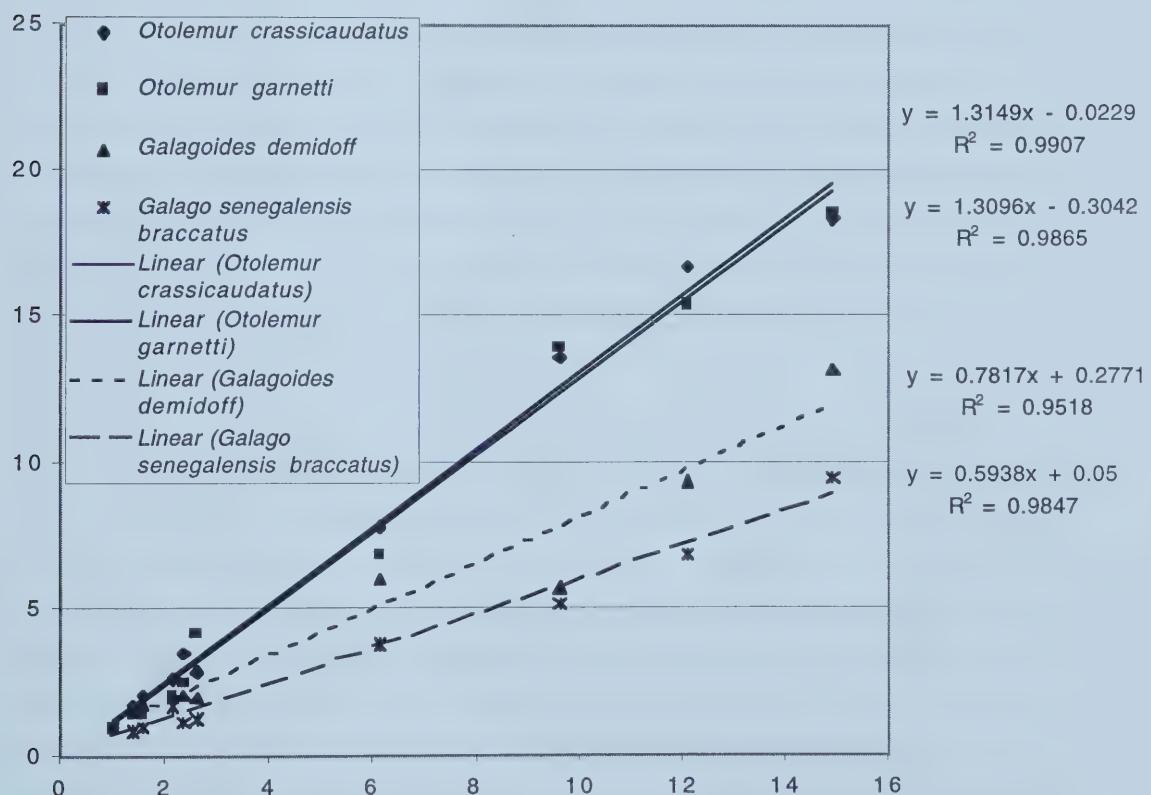


Figure 5-6 Relative muscle strength in each species plotted against mean relative muscle strength. Each point represents the relative muscle strength for one muscle for a given species. Each species is represented by a different shape. A linear regression trendline (with equation and R-squared value) is shown for each series (i.e., each species). Four different shapes line up in a column for each muscle. The muscles are plotted in order of increasing strength, left to right.

the temporal. The temporal is proportionately strongest in *Papio*, *Mandrillus* and galagids (more than 50% of the strength in the masticatory complex). The pterygoid muscles are very weak in galagids, much more so than those in the other primates. Perhaps this is due to the more orthal movement of the mandible during chewing in galagos, as compared to all other primates measured. In fact, the relative strength of the pterygoids in galagids is most comparable to that seen in the rat. The pterygoids are proportionately strongest in humans.

5.4.5 *Implications for individual species within the Galagidae*

5.4.5.1 *O. crassicaudatus*

The diet of *Otolemur crassicaudatus* is well-studied in the wild. However, the results of different studies differ, possibly because different methods were used to determine diet (Cordell, 1991). Most studies present data on the percentage of time spent consuming various kinds of food. According to these studies, *O. crassicaudatus* spends the greatest portion of its feeding time on gums (Charles-Dominique and Bearder, 1979; Harcourt, 1980). Not only does it consume fresh, liquid gum, but it also consumes gum that has dried to the “consistency of toffee” (Charles-Dominique and Bearder, 1979, p. 612). This species also spends a lot of time consuming insects and fruit; however, the importance of fruit vis-à-vis insects is uncertain (see Cordell, 1991). *O. crassicaudatus* has been observed consuming nectar as well (Coe and Isaac, 1965, in Sussman, 1978).

Among galagos, *Otolemur crassicaudatus* possesses stronger than average superficial masseter, superficial temporal and zygomatic temporal muscles. This suggests both an adaptation to strong vertical forces in mastication, as well as the potential for significant retraction of the mandible. The acquisition and processing of gum can account for both of these. Galagos rely on the action of wood-boring insects to stimulate the production of gum in acacia trees. However, galagos often peel back the bark of the acacia tree with their caniniform lower premolars to gain access to additional gum (Bearder and Martin, 1980). This retractile action requires that strong forces concentrate on the anterior part of the dentition. Strong temporal muscles (especially the zygomatic temporals) benefit an animal that performs this kind of action regularly.

O. crassicaudatus often feeds on dried gum. Feeding on a tough, but soft toffee-like material like dried gum requires that strong forces be sustained in the dorso-ventral plane during mastication. The majority of the fibres of the superficial temporal have a strongly dorso-ventral orientation. As well, both the superficial temporal and the superficial

masseter are very large muscles that act to elevate the mandible. Hypertrophy of both of these muscles is beneficial in processing dried gum.

5.4.5.2 *Otolemur garnetti*

O. garnetti consumes mainly fruit, but also eats a large quantity of insects (Harcourt, 1984; Harcourt and Nash, 1986) and some birds (Harcourt and Nash, 1986). This species is probably the most frugivorous of the galagids studied here. It does not consume gum; gum-producing trees are absent from its range (Harcourt and Nash, 1986).

The superficial temporal and the deep masseter are highly developed in this species. This is consistent with strong vertical forces generated during mastication of hard fruits. However, the zygomatic portion of the temporal is weak: mandibular retraction is less important in this species as it abstains from gummivory. The pterygoid muscles are also particularly weak in this species. This suggests that this species has little need for strong transverse forces during mastication. This suggestion is consistent with a frugivorous-insectivorous habit.

5.4.5.3 *Galago senegalensis braccatus* and *Galago demidoff*

Though *Galago senegalensis braccatus* is poorly studied, it is thought to eat mostly insects, some fruit and some gum (Nash, 1989; Haddow and Ellice, 1964, in Cordell, 1991). The diet of *Galago demidoff* is very similar (Charles-Dominique, 1977; Charles-Dominique and Bearder, 1979).

Not only are these two species similar with respect to diet, but they are similar with respect to relative muscle strength (see Figure 5-6). In both species, the deep temporal, the zygomaticomandibular and the medial pterygoid are stronger than average. The superficial and zygomatic temporal, as well as the superficial and deep masseter are weaker than average. I am unable to suggest a functional explanation for this variation, other than that both species are eating similar foods in similar proportions and both show the same pattern in relative masticatory muscle strength. Perhaps they are eating weaker foods than the other galago species. It is possible – though untested - that this pattern is due to phylogenetic constraints. This is difficult to interpret without prior knowledge of the plesiomorphic condition of relative strengths of masticatory muscles in galagos. The especially strong muscles are all very deep, whereas the weak ones are superficial.

5.5 Conclusion

Prior to this study, the physiological cross-sectional areas of the muscles of mastication in galagids were unknown. Furthermore, no electromyographic test has been performed successfully on these muscles during chewing. Therefore, no data were available for use in estimating the relative masticatory forces generated by these muscles. I performed this study because I required such an estimate to produce a realistic simulation of mastication. This study also gave me the opportunity to measure the orientation of muscle fibres and locate the origins and insertions of masticatory muscles on cadavers. This is particularly important as the reconstruction of muscles from skeletal elements alone can be misleading (Bryant and Seymour, 1990).

In the course of my study of galagid masticatory muscles, I discovered variation in muscle strength both within and between species. For most of this variation, there is a corresponding functional explanation related to dietary preference. *O. crassicaudatus* consumes hard gum in large quantities and possesses very strong masticatory muscles that aid in obtaining and processing gum. Those masticatory muscles that generate the most force in the vertical plane are the strongest in *O. garnetti*; this may have some relationship to the breakdown of hard fruits and insects. Perhaps the other two galago species consume softer, less resistant foods: they possess relatively weaker muscles of mastication. The relationship between masticatory muscle architecture and diet is still poorly understood. Further study in this area would enhance our understanding of this relationship in galagids and prosimians in general.

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Chapter 6: The mastication machine

6.1 Introduction

Our insight into the past relies on our knowledge of the present. Studies of functional morphology contribute to our understanding of past faunas: they allow us to make hypotheses about extinct animals based on physical principles that we assume have remained constant throughout time. Many hypotheses can be generated based on mathematical models (Gingerich, 1972; Greaves, 2000). However, for complex systems such as the mechanism responsible for food breakdown in extinct primates, a more complex approach may be instructive. One such approach is biomechanical simulation.

Even without the use of robotics it is possible for functional morphologists to simulate many behaviours (Brace and Molnar, 1967; Wells *et al.*, 1982; Weishampel, 1993; Naples, 1995). One can imagine many ways of simulating mastication in extinct primates. To my knowledge, no one has ever before attempted to simulate mastication in a nonhuman primate using a machine. Brace and Molnar (1967) built a machine to simulate *human* mastication for the purpose of determining why certain characteristic patterns of tooth wear occur in aboriginal populations. However, that machine chewed no actual food, rather it generated wear by tooth-on-tooth contact. Brace and Molnar's study inspired me to simulate true chewing in extinct primates. The design for my machine owes a great deal to their design.

It would be interesting to simulate the mastication behaviour of a single extinct primate and observe how it breaks down various foods. However, it is more significant to do this for several species and compare their performances. It would be very time-consuming to build one machine for each species; therefore, I chose one extant model upon which to base it.

A few factors must be kept in mind when choosing a good model for such a machine. Its masticatory behaviour should be well known. This restricts us to a few species of mammals and even fewer species of primates (Hiiemae, 1978; Hylander, 1979; Fish and Mendel, 1982; Callum and Wall, 2000). Its masticatory apparatus should be morphologically similar to the extinct species in question - assuming that similar morphology often indicates similar function. The mammal that best qualifies given these two criteria is the thick-tailed bushbaby, *Otolemur crassicaudatus* (Primates: Galagidae).

Mastication in *Otolemur crassicaudatus* is well-studied (Minkoff, 1968; Cordell, 1991; Hiiemae and Kay, 1973; Kay and Hiiemae, 1974a and b; Hylander, 1977; Hiiemae, 1978; Hylander, 1979; Hylander *et al.*, 1998; Chapter 5, this study) and the dental and

cranial morphology of the Galagidae resemble those of some of the earliest primates. In fact, the Galagidae contains some of the most primitive living prosimians.

The galagids are behavioural generalists. They have many dietary, metabolic and morphological characteristics that are probably primitive retentions from the earliest prosimians. The first prosimians (and probably the first primates) were probably nocturnal tree-dwellers that lived on a variety of foods including insects and fruits, much like extant galagids (Charles-Dominique, 1977, pp.257-259; Charles-Dominique and Martin, 1985; Rasmussen and Nekaris, 1998). These facts support the use of a galagid as a model for mastication in early primates (Charles-Dominique, 1977).

Many (Le Gros Clark, 1959; Simpson, 1945; Abplanalp, 1971; Goode and Haines, 1975) have suggested that tree shrews should be considered the most primitive living primate or a transitional form between Primates and Insectivora. Moreover, some have used *Tupaia glis* as a living analogue for the earliest primates (Abplanalp, 1971; Goode and Haines, 1975) or have suggested that it is the best living analogue for the extinct Plesiadapiformes (Le Gros Clark, 1959). However, the “family Tupaiidae does not appear to share any uniquely derived character states with Primates” (Luckett, 1980) and they are now assigned to their own order, Scandentia (Butler, 1980; Luckett, 1980). Tree shrews are probably more distantly related to extant primates than are plesiadapiforms and the features they share with primates are now thought to be primitive characters of archontans (=Scandentia, Primates, Dermoptera + Chiroptera and perhaps elephant shrews) (Luckett, 1980; Simmons, 1993). For this reason, and because their mastication behaviour is less well-known than that of *O. crassicaudatus*, I have refrained from using a tree shrew as a model for my machine.

6.2 Construction details

Good scientific experiments are replicable. Replication is the only way for others to refute one’s data. Therefore, I will describe the construction of my mastication machine in chronological order and fine detail to help others build similar machines. The mastication machine is depicted in Plates 3 and 4.

6.2.1 The frame

On a wooden base, 22" long, 16" wide and 3/4" thick¹, I built a frame 13.5" long x 13.5" wide x 12" tall. Each post in the frame is 12" long x 0.75" wide x 0.75" thick. These posts were joined together using steel brackets.

On either side of the frame, I affixed a wooden cross-bar (also 12 x 0.75 x 0.75) to the front and back upright posts, at 5" above the base, in the horizontal plane. I wedged a pressed-board panel between the cross-bar and the horizontal post above. Each panel is 4.75" tall x 7.75" long x 0.75" thick.

Drilled into each panel are four holes I will call A, B, a and b. Holes A and B are 1 3/4" in diameter. Their centres are both at 10" above the base of the frame and 4.75" from the front of the frame² for A and 4 5/16" from the back for B. Holes a and b are 5/16" in diameter. Their centres are both at 9 3/8" above the base of the frame and 3.75" from the front of the frame for a and 3.5" from the back for b. As the machine is bilaterally symmetrical, there is a hole A-right and a hole A-left, B-right and B-left, etc.,³ for a grand total of eight holes.

A 1 3/8" diameter, 5/8" bore steel flange bearing is inserted into each of the A and B holes and is cemented in place using silicone sealant.

A 12" long, 3/4" thick, 3/4" wide wooden bar is screwed into the right and left cross bars directly anterior to the anterior border of the right and left side panels. This bar sits in the frontal plane and is referred to as the anterior cross bar. It is 6" above the base and 2 1/2" from the front of the frame. It holds several pulleys. A similar cross bar holds the pulleys for the posterior cables; it is referred to as the posterior cross bar and it is 6" above the base and 2 1/2" from the *back* of the frame.

6.2.2 The cams

A cam is a rotating wheel that looks egg-shaped when viewed from the side. The bulge that constitutes the top of the egg is called the 'high side' of the cam. Like any wheel, a cam has a hole in its centre through which a shaft (i.e., the camshaft) runs. As the shaft

¹ The Imperial system of measurements is universal in hardware stores and machine retailers in Canada; all my original building materials are cut in inches and feet. Therefore, despite the fact that all other measurements in this thesis are in metric, I have used inches and feet for this chapter.

² All measurements referring to the front, back or sides of the frame are measured from the *outside* edge of the frame. All measurements referring to a 'side' designate either the left or the right side, never the front or the back.

³ The terms 'right' and 'left' always refer to the animal's (i.e., *O. crassicaudatus*) right and left sides.

turns under the power of a motor, the cam turns as well. The cam does nothing during most of its rotation, until its high side collides with some object and moves it. In my machine, each cam collides with a ‘rocker arm’.

I shaped fourteen cams for my machine, one pair for each pair of muscles simulated. Each cam is 0.25” wide. Each has a minimum diameter of 5/16”, though maximum diameters vary depending on the load I wish it to apply. Through the centre of each cam, I drilled a 5/16” bore to house a 5/16” steel camshaft.

One side of each cam is glued (using G2 epoxy glue – available from Industrial Formulators of Canada Ltd., Burnaby, B.C.) to a 5/8” diameter, 5/16” bore aluminum sleeve equipped with a set screw. The bore in the sleeve is aligned with the bore in the cam so as to accommodate the passage of the 5/16” steel camshaft.

The specifications for each cam are given in section 6.3.

6.2.3 *Camshafts*

Eight cam+sleeve units are attached to a 5/16” diameter, 18” long steel camshaft by tightening the set screws on the sleeves. The cams are spaced apart at 1.5” intervals. The right-most cam is affixed 1 7/8” from the right side of the frame. This is the anterior camshaft.

Six cam+sleeve units are attached to a 5/16” diameter, 18” long steel camshaft by tightening the set screws on the sleeves. The cams are spaced apart at 1.25” intervals. The right-most cam is affixed 3 1/2” from the right side of the frame. This is the posterior camshaft.

The anterior camshaft is inserted into the frame of the machine, though hole A on the right and left, leaving 1 3/4” of the shaft projecting beyond the right side of the frame and 2 3/4” projecting beyond the left side. A sleeve with a 5/8” diameter, and a 5/16” bore is screwed to either side at the level of the flange bearings. The outsides of the sleeves are cemented with silicone sealant to the insides of the bearings.

The posterior camshaft is inserted into the frame of the machine, though hole B on the right and left, leaving 1 3/4” of the shaft projecting beyond the right side of the frame and 2 3/4” projecting beyond the left side. A sleeve with a 5/8” diameter and a 5/16” bore is screwed to either side at the level of the flange bearings. The outsides of the sleeves are cemented to the insides of the bearings.

A steel collar, 1 1/16” diameter and 5/16” bore, is screwed (via set-screw) to each shaft, beyond the left-hand side of the frame. Each of these collars is glued to a # 41 sprocket with 14 teeth. The two sprockets are linked together by a size 11 chain with 32

links. The purpose of the chain assembly is to synchronize the rotation of the two camshafts.

6.2.4 *Motor assembly*

The machine is powered by a 1/150 horse power motor (Bodine Electric Company, Chicago, USA) that sits to the right of the machine. It turns a 5/16" shaft at 300 r.p.m. (rounds per minute). The motor shaft projects toward the machine in the frontal plane and turns counterclockwise (if you face the right side of the machine).

A double-sheave, v-belt pulley wheel (type A22, 4 1/8" narrowest circumference, 5/8" bore) is screwed to the motor shaft and turns with it. Into the groove of each sheave (one on the left and one on the right) fits an A26 v-belt. The opposite end of each v-belt fits into the groove of another pulley wheel, one attached to the anterior camshaft and the other attached to the posterior camshaft. Each of the latter pulley wheels is singly sheaved. Each is a type A and has a narrowest circumference of 6.5". All pulley wheels described here attach to a shaft through the use of a set screw.

The first single-sheave pulley wheel is screwed to the posterior camshaft such that the centre of the v-belt it houses is 1 5/8" beyond the right side of the frame. This pulley wheel sits directly above the right-most sheave of the motor's pulley wheel, such that the v-belt runs in the vertical plane. The other single-sheave pulley wheel is screwed to the anterior camshaft such that the centre of the v-belt it houses is 7/8" beyond the right edge of the frame. This pulley wheel sits directly above the left-most sheave of the motor's pulley wheel, such that the v-belt runs in the vertical plane.

When the motor is activated, its 300 r.p.m. shaft turns counterclockwise. This turns the attached double-sheave pulley wheel at 300 r.p.m.; that, in turn, causes both v-belts to turn at 300 r.p.m. counterclockwise. Each v-belt turns the single-sheave pulley wheel at its opposite end; that, in turn, causes a camshaft to turn. As the camshafts turn, the high ends of the cams are brought to bear.

As the circumference of the double-sheave pulley wheel is less than that of each single-sheave wheel, the camshafts turn more slowly than the motor shaft. The circumference of the motor shaft pulley wheel is 4.125" and that of the camshaft pulley is 6.5". The motor shaft pulley wheel turns at 300 r.p.m., therefore one revolution (i.e., one full chewing cycle) takes 0.20 seconds. The time it takes for the camshafts to make a single revolution is determined by the following:

$$= 0.20 \text{ seconds} \times 6.5" / 4.125"$$

$$= 0.31515 \text{ seconds} = 0.32 \text{ seconds}$$

This converts to 190.38 r.p.m. = 1.9×10^2 r.p.m.

Therefore the chewing cycle simulated by the machine takes approximately 0.32 seconds to complete.

As the friction induced by each camshaft is different, one v-belt tends to slip on its pulley wheel, and the camshafts become asynchronous. To simulate chewing properly so that one rotation is equivalent to one full chewing cycle, all cams must turn at the same rate. Therefore, I added the chain assembly to the left side of the camshafts. The chain and sprockets keep the two camshafts in time with one another.

6.2.5 *Rocker assembly*

Through each of holes a and b of the right and left wood panels is threaded a 5/16" diameter, 14" long steel rod. These become the rocker shafts. Onto the anterior rocker shaft (holes a on the right and left sides) are threaded eight rocker units: one rocker unit for each cam. The posterior rocker shaft holds six rocker units: again, one rocker unit for each cam.

Each rocker unit consists of three components: a rocker arm, an aluminum sleeve (5/8" diameter, 5/16" bore, with a set screw), and a bearing (1 3/8" diameter, 5/8" bore).

The rocker arm is a 3" long, 1/2" wide, 1/2" thick wooden block with a 5/16" hole drilled through its width at 1" along its length. The anterior rocker arms slide onto the 5/16" rocker shaft such that 1" of the block's length projects posteriorly from the shaft and 2" project anteriorly. Another 5/16" hole is drilled through the long end of each rocker arm, 1.5" anterior to the centre of the rocker shaft. This hole is drilled dorso-ventrally. A steel eye bolt (4" long, 2 3/4" thread length, 1/4" diameter at the threads) is threaded vertically through this hole. The six posterior rocker arms mirror the eight anterior ones: 2" of the arm projects posteriorly; 1" projects anteriorly.

The left side of each rocker arm is cemented to a bearing at the bearing's outer circumference. The inner circumference of each bearing slides over-top of an aluminum sleeve and is cemented to its outer circumference. The bearings equalize the rotation of the wooden rocker arms.

As each cam turns, its high side contacts the short end of a rocker arm and forces its long end to swing upwards like a lop-sided teeter-totter. When this occurs, the eye bolt at the long end of the rocker arm rises. A 1/48" thick steel cable is looped into the eye of

each eye bolt; these cables represent the muscles of mastication. When an eye bolt rises, a pulling force is exerted on the attached cable. Eye bolts can be loosened to reduce this pulling force, or they can be tightened to increase it. This feature is useful for approximating biologically realistic relative mastication. Figure 6-1 is an illustration of a single simulated muscle. It depicts a single cam with attendant rocker arm and cable.

6.2.6 Cables

The machine uses fourteen cables to simulate the action of seven pairs of masticatory muscles. Every effort has been made to replicate the magnitudes and directions of the forces of galago jaw muscles.

The four basic mammalian muscles of mastication are the following: masseter, temporal, pterygoid and digastric. For the purposes of this study, the temporal is divided into two functional units: the superficial temporal with a more dorso-ventral orientation and the deep temporal with a more antero-posterior orientation. The masseter is divided into two functional units: the superficial masseter, with a more antero-posterior orientation and the deep masseter, with a more dorso-ventral orientation. The pterygoid is also divided into two functional units: the medial pterygoid and the lateral pterygoid. The justification for establishing these functional groups and a detailed explanation of chewing muscles in *Otolemur crassicaudatus* are provided in Chapter 5.

Each muscle is simulated by a cam that operates on a rocker, that in turn pulls a single cable. Each cable used to simulate a muscle is the result of un-braiding a larger (1/16") steel aircraft cable. A 1/16" cable is composed of six 1/48" cables braided around a central 1/48" cable. I have used the central cable for my machine as a 1/48" diameter cable is flexible enough to be redirected over pulleys to approximate the orientation of chewing muscles. The 1/48" cable also resists being bent permanently.

6.2.6.1 Medial pterygoid

The central cams, rockers and cables of the anterior shafts simulate the action of the paired medial pterygoid muscle. From its 'origin' on the eye bolt, each cable runs down to the anterior cross bar and passes under a pulley that angles it medially, posteriorly and ventrally. This pulley is screwed to a small wooden bar (2" long) that projects anteriorly from the anterior cross bar; the pulley hangs postero-medially from the underside of the bar. The pulley is attached 1 1/2" anterior to the anterior cross bar. The left and right medial pterygoid cables cross over one another directly above the snout of the galago skull,

just anterior to the orbits. The right-hand cable inserts on the medial surface of the angle of the left mandible. This becomes the *left* medial pterygoid muscle⁴.

6.2.6.2 Lateral pterygoid

The eye bolts that simulate the lateral pterygoid muscles are lateral to those that simulate the medial pterygoid muscles. Each lateral pterygoid cable runs from its eye bolt, down beyond the anterior cross bar to a 2 3/8" x 3/4" x 3/4" wooden post that is attached - just inside the anterior border of the frame - to the wooden base. The cable runs under a pulley that is screwed to the top of the 2 3/8" post. This pulley is situated 9/32" from the front of the frame and 4 1/4" from the nearest side of the frame; it angles the cable posteriorly as well as medially and it projects dorso-medially from the top of the vertical post. The right lateral pterygoid crosses the left lateral pterygoid below the mandible. The right-hand cable passes just under the inferior border of the horizontal ramus of the right side of the mandible to insert on the antero-ventral border of the left mandibular condyle. This cable becomes the *left* lateral pterygoid.

6.2.6.3 Deep masseter

The cables for the deep masseter originate at a more lateral position. Each runs ventrally toward the anterior cross bar and runs under a pulley. This pulley is attached to a small wooden bar that projects anteriorly from the anterior cross bar; the pulley hangs postero-medially from the underside of the bar. The cable encounters this pulley 3/8" anterior of the anterior cross bar and 3 1/8" from the closest side of the frame. The pulley angles the cable medially, ventrally and posteriorly. The right cable runs over the dorsal surface of the zygomatic process and descends medial to the zygomatic arch, inserting on lateral surface of the right mandible within the masseteric fossa.

6.2.6.4 Superficial masseter

The cables for the superficial masseter originate at the lateral-most position on the anterior rocker shaft. Each runs ventrally toward the anterior cross bar and runs under a pulley. This pulley is attached to the same small wooden bar as the deep masseter and hangs postero-ventrally from the lateral side of the bar. The cable encounters this pulley 1 1/4" anterior of the anterior cross bar and 2 3/8" from the closest side of the frame. The pulley angles the cable medially, posteriorly and ventrally. The right cable runs lateral to the

⁴ All muscle cables are inserted into tiny holes drilled into the epoxy mandible. They are held in place by G2 epoxy reinforced with fiberglass strands.

lateral surface of the zygomatic process and inserts on the lateral surface of the right mandibular angle.

6.2.6.5 Digastric

The cables representing the digastric muscles originate at a medial position along the posterior rocker shaft. Each runs ventrally, underneath a pulley. Each pulley is screwed to the top of a small vertical post (2" tall) and projects dorsally from the posterior side of the post. The cable encounters the pulley at a point 5 3/8" from the nearest side. The pulley redirects the cable so that it runs horizontally to the anterior of the machine. The right-hand cable passes just medial to the medial surface of the mandibular angle and inserts on the medial aspect of the right horizontal ramus at about the level of the p3.

6.2.6.6 Deep temporal

The cables representing the deep temporals originate laterally to those for the digastrics. Each runs ventrally and courses under a pulley that is screwed to the underside of the posterior cross bar. The pulley projects anteriorly from the posterior cross bar and angles the cable anteriorly and medially. The cable encounters the pulley at a point 4 3/4" from the nearest side. The right cable crosses over the left behind the epoxy skull at a point 3" above the base, 5 1/2" from the front of the frame and 6" from either side. Beyond that point, it passes forward to insert onto the anterior border of the left coronoid process of the mandible and becomes the *left* deep temporal.

6.2.6.7 Superficial temporal

The cables for the superficial temporals originate at the lateral-most position on the posterior rocker shaft. Each runs ventrally and courses under a pulley that is screwed to the underside of the posterior cross bar. The pulley projects anteriorly from the posterior cross bar and angles the cable anteriorly and medially. The cable encounters the pulley at a point 3 1/2" from the nearest side. The cable continues antero-medially and then passes over another pulley at a point 3 1/2" above the base, 5 1/2" from the front and 6 1/4" from the nearest side. This second pulley projects dorsally from the top of a 3 1/2" vertical post and angles the cable ventrally and further medially. Just anterior, the right cable crosses over the left. Beyond that point, it passes forward to insert onto the lateral aspect of the left coronoid process of the mandible and becomes the *left* superficial temporal.

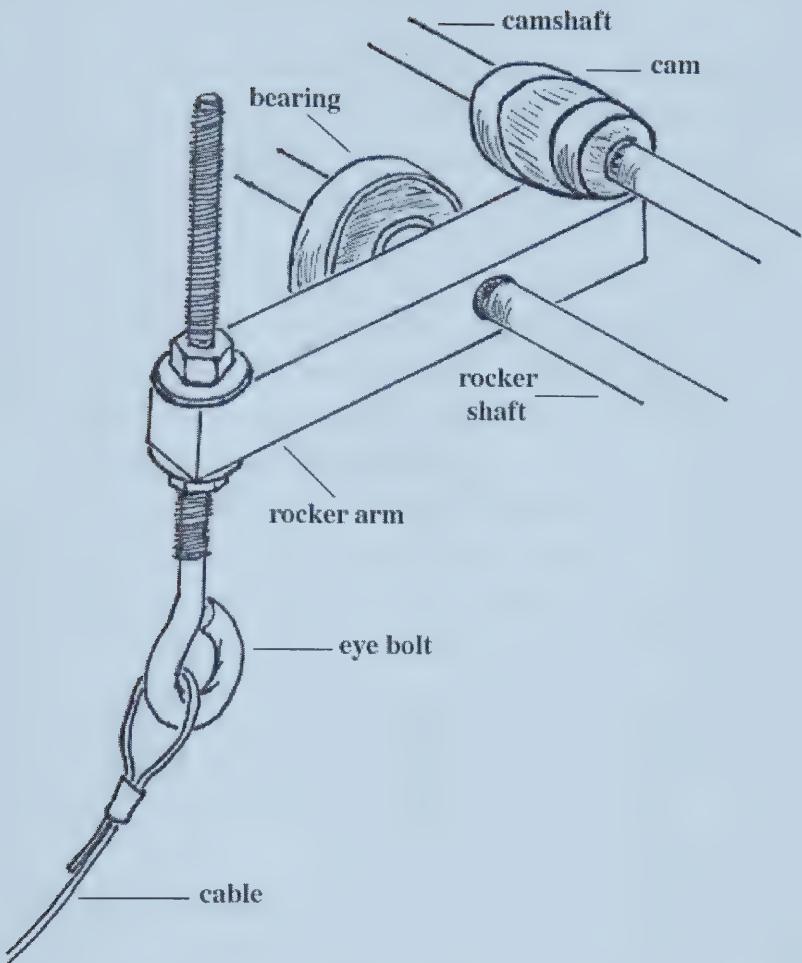


Figure 6-1 Diagram of a single moving unit of the mastication machine. Each muscle is simulated using a unit like this one. See the description of individual parts for scale.

6.2.7 The skull and teeth

At the centre of the frame, one end of a 5/16" diameter 3 1/16" long steel rod is rooted to the wooden base. At its other end, the steel bar is glued into the foramen magnum of an epoxy cast of a skull of *Otolemur crassicaudatus*. The upper and lower teeth of this specimen have been sanded down entirely, leaving a flat surface for the attachment of prosthetic tooth rows.

I cast the upper and lower tooth rows of seventeen primate species (plus *Tupaia glis*) in methyl-methacrylate. These tooth rows consist of the two posterior premolars and all the molars of a single maxilla and the p3 through m3 of a single dentary, from either the right or the left side. Each tooth row is sanded flat proximally, allowing for a solid bond between the tooth row and the maxilla/mandible.

Tooth rows can be bonded to the skull or mandible (i.e., ‘installed’) quickly and easily using silicone sealant. Unlike epoxy, silicone is easily removed.

I also made two artificial ‘tooth rows’ for testing in the machine. One is entirely flat. The other is an array of simple points, cast from the heads of nails, arranged in the configuration of cusps that is common to early fossil primates. Only the major cusps are represented. The purpose of testing these artificial dentitions is to examine the role of cusp acuteness in food breakdown: the ‘flat’ dentition is one extreme (i.e., the least acute cusps possible) and the ‘pointy’ dentition is the other (i.e., the most acute).

6.3 Muscle parameters

In order to simulate mastication in a primate like *Otolemur crassicaudatus*, it is necessary to know a number of physical details of its jaw musculature (i.e., levators and depressors of the mandible). Fortunately, much is known about these muscles in *O. crassicaudatus*. This is because there are many thick-tailed bushbabies in captivity, and because galagids are often considered good analogues for the earliest primates (Charles-Dominique, 1977; Rasmussen and Nekaris, 1998).

It is possible to subdivide any muscle to near-infinity when attempting to isolate functional muscle components. However, I have chosen to simulate seven muscles: five that raise the mandible, one that lowers it and one whose action in living bushbabies is uncertain.

The lateral pterygoid muscle is considered as a depressor, a levator or a stabilizer of the mandible during chewing (McNamara, 1973; Hatcher *et al.*, 1986). Some of this uncertainty is attributed to the difficulty in reliably inserting an electrode into this muscle in a live animal (Hylander *et al.*, 1987). The magnitude of force imposed on the mandible by

the lateral pterygoid is very small in proportion to that of the other muscles I simulated; therefore, no matter how I simulate it, its effect is minimal. However, it performs as a mandibular depressor and stabilizer in my machine as it peaks at the end of centric occlusion. The actions of particular muscles and their anatomical characteristics are further detailed in Chapter 5.

The duration of the chewing cycle has been recorded for several mammals including bats (Kallen and Gans, 1972; De Gueldre and De Vree, 1988), *Rattus norvegicus* (Byrd, 1988), *Tupaia glis* (Fish and Mendel, 1982), *Macaca mulatta* (Luschei and Goodwin, 1974), *Macaca fascicularis* (Hylander, 1979), *Homo sapiens* (Bates *et al.*, 1975) and most importantly *Otolemur crassicaudatus* (Hiiemae and Kay, 1973; Kay and Hiiemae, 1974a; Hylander, 1979). Hiiemae and Kay (1973) estimated that the chewing cycle in *O. crassicaudatus* lasts 314.5 milliseconds (+/- 47 ms). Kay and Hiiemae (1974a) suggested 374 ms and Hylander (1979) suggested 1/3 - 1/2 s; however, the former (374ms) is a number I calculated from a representative diagram, rather than an explicitly stated value. The latter (1/3-1/2s) is not accompanied by supporting statistics.

I chose to emulate the value given in Hiiemae and Kay (1973), because the authors accompany it by statistical support and because they state the number of individuals represented by the average chewing cycle length. My machine produces a chewing cycle that is 315.15 ms long (see Section 6.2.5). This is very close to the cycle length suggested by Hiiemae and Kay (1973).

The orientations of the jaw muscle forces in *O. crassicaudatus* are poorly studied. They are described very basically by Murie and Mivart (1872), by Minkoff (1968) and by Cordell (1991) but precise angles for muscle fibres are not published. To simulate the action of the chewing muscles of *O. crassicaudatus*, it was necessary to estimate the orientations of the forces involved. To estimate these, I used diagrams in Murie and Mivart (1872) and in Cordell (1991) together with orientations I obtained from a cadaver of *O. crassicaudatus* (see Chapter 5). Cordell (1991) suggested that the true orientation of a muscle of mastication can be estimated by drawing a line (in three dimensions) between the site of origin and the site of insertion of that muscle. This works well for a thin tendon-like muscle with a restricted origin and insertion, but it fails when: A. the muscle in question has a large site of insertion or origin or B. the muscle curves along its length. Thus, the reconstruction of muscle orientations from skeletal material alone is often problematic (Bryant and Seymour, 1990). Therefore, I measured the orientations of muscle fibres in the muscles of mastication directly on a preserved (in ethanol) head of *O. crassicaudatus*. In the case of the temporal muscle, which curves markedly along its length, even a direct measurement of orientation must be regarded as a gross approximation.

Table 6-1 shows the direction of pull of the simulated muscles in my machine. To generate transverse movements of the mandible, it was necessary in some cases to increase the angle of pull (in the horizontal plane 'x') of simulated muscles beyond the measured orientations of *O. crassicaudatus* muscles (see Table 5-1).

The relative magnitudes of force generated by the jaw muscles during chewing in *O. crassicaudatus* were, hitherto, unmeasured. Absolute jaw muscles forces have been recorded using electromyography (or EMG) in humans (Hatcher *et al.*, 1986), but not in bush babies. A simple procedure for estimating the *relative* forces of muscles, described in

muscle	side	apparent angle of pull – x ¹	apparent angle of pull – y ²	magnitude of pull ³	timing of peak activity ⁴	duration of peak activity ⁵
Superficial masseter	working	60	55	424	290	20
	balancing	60	55	212	330	20
Deep masseter	working	45	63	172	300	20
	balancing	45	63	142	320	20
Lateral pterygoid	working	80	-15	60	0	20
	balancing	80	-15	44	0	25
Medial pterygoid	working	25	55	200	340	25
	balancing	25	55	150	280	25
Superficial temporal	working	27	145	512	300	20
	balancing	27	145	472	300	20
Deep temporal	working	33	165	473	300	20
	balancing	33	165	426	300	20
Digastric	working	15	-175	83	120	33
	balancing	15	-175	83	120	33
Duration of one chewing cycle...		Total vertical load on mandible...				
for machine:		for machine:				
for <i>O. crassicaudatus</i> :	314.50 ms	approx. 1.476 kg				

Table 6-1 Parameters for cams. ¹Measured as the smallest angle to the sagittal plane. ²Measured from the horizontal plane. Negative value means below horizontal plane. Value greater than 90 degrees means posterior orientation. Angles are estimated from osteological specimens (hence the deviance from those in Table 5-1). Values for the superficial temporal are composites of those for the superficial temporal and the zygomatic temporal of Table 5-2. Values for the deep masseter are composites of those for the deep masseter and the zygomaticomandibular of Table 5-2. Values for the digastric are composites of those for the anterior digastric and posterior digastric of Table 5-2. ³In grams. ⁴In degrees. Centric occlusion ends at 0 degrees. ⁵As a percentage of the total chewing cycle.

Chapter 5, relies on the physiological cross-sectional area (or PCS) of several muscles. The use of PCS to estimate relative muscle forces requires the following assumption: the cross section of a muscle is directly proportional to the force that muscle generates during ‘normal’ activity⁵. I measured the PCS of the chewing muscles in one individual of *O. crassicaudatus*. I used these to estimate forces for the muscle cables in my machine (see Table 6-1). For comparison, I measured the PCS of the masticatory muscles of seven more individuals (representing a total of four species) of the bushbaby family (see Chapter 5). PCS is an estimate of only those forces generated during normal activity (i.e., chewing); therefore, it can only be used to estimate the forces generated by the *working* muscles, not the balancing muscles. Values for the balancing muscles can be estimated only from living animals (using EMG). This has not been done for *O. crassicaudatus*, therefore I varied the magnitudes of force generated by the simulated balancing muscles until I achieved a realistic chewing motion. These values are also shown in Table 6-1.

To measure the relative forces generated by the muscle cables in my machine, I used a small custom-made scale (Figure 6-2). A small spring inside the scale lengthens when a weight is applied to one end. Barring manufacturing imperfections, the length of the spring varies constantly with the weight placed upon its moving end. This instrument was calibrated repeatedly using weights of known mass. One end of the scale was anchored to the distal end of the skull post (the skull was removed for this procedure), and the other was attached to the distal end of a muscle cable. The machine was activated and the maximum force (in grams) was recorded from a display on the scale. The scale measured up to 0.5 kg of force and it was accurate to a hundredth of a kilogram.

The PCS of the jaw muscles is an estimate of the forces they generate. However, I wanted to reproduce the masticatory behaviour of *O. crassicaudatus* as faithfully as possible. Therefore, I needed to have some estimate of the *absolute* forces it produces during mastication. Hylander (1979) measured the mean unilateral vertical bite force of three thick-tailed bushbabies at 6.9 kg at a single site on the working side of the mandible. Due to the uncooperative nature of the subjects, he was unable to measure forces during chewing, but he suggested such forces are approximately one-quarter of those generated during biting. This ratio is the result of studies on humans (Bates *et al.*, 1975). The

⁵ Physiological cross-sectional area should give the (relative) force that a muscle generates during its ‘normal’ activity, rather than those forces generated during strenuous or abnormal activity. For the muscles of mastication, chewing is the normal function; biting requires much more force and different relative forces than does chewing.

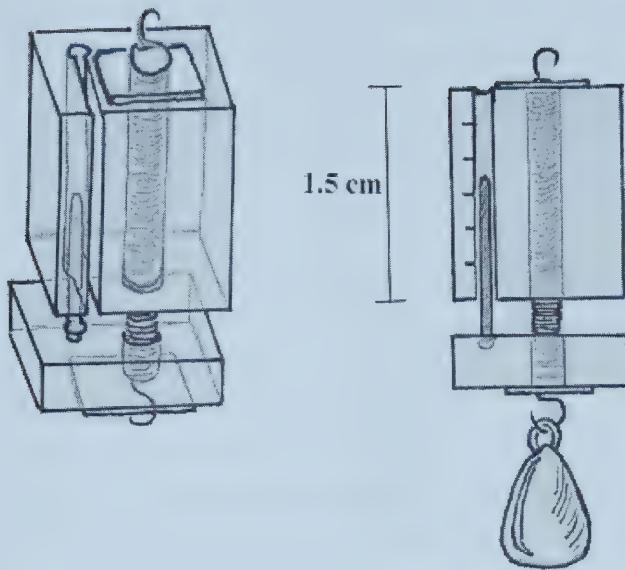


Figure 6-2 Custom scale. Scale used to measure the force generated by simulated muscles in the mastication machine. See text for description.

resulting estimate for absolute chewing force in *O. crassicaudatus* is 1.8 kg.

Using vector geometry, with the magnitudes and orientations of force of the individual muscles as variables, I calculated the total vertical force applied to the mandible by all the muscle cables combined. The resulting value is 1.5 kg (see Table 6-1). Therefore, the forces generated by my machine are somewhat weak compared to those generated by Hylander's three bush babies, but they are within reason. I attempted to increase the forces in the machine, but found that this caused a considerable increase in friction between the moving parts. The corresponding value for humans is between 0.4 kg and 3.075 kg (Bates *et al.*, 1975) and that for *Macaca fascicularis* is 2 kg (Hylander, 1979). I attempted to increase the total force generated by the muscle cables, but this increased to dangerous levels the friction between moving components.

The timing and duration of peak muscle activity are crucial to the configuration of the cams in my machine. The orientation of a cam within the rotation of the camshaft (relative to the other cams) is determined by the timing of the peak activity of the muscle represented by the cam (relative to the timing of the peak activity of the other muscles represented). As the camshaft rotates, the cam whose high side impacts on its rocker arm first should be the jaw muscle that experiences peak activity first.

The timing and duration of peak activity of the masticatory muscles in *O. crassicaudatus* have not been studied. Therefore, it is necessary to estimate these values

from studies of other mammals. The masticatory muscles of the little brown bat, *Myotis lucifugus*, and those of the flying fox, *Pteropus giganteus*, have been quantified as to the timing and duration of peak activity (respectively, Kallen and Gans, 1972; De Gueldre and De Vree, 1988). I estimated timing and duration of peak muscle activity from Kallen and Gans (1972) and De Gueldre and De Vree (1988) then averaged and rounded them to estimate corresponding values in *O. crassicaudatus*. The values I chose for my machine appear in Table 6-1. Although these parameters have been studied in *Homo sapiens*, a primate, the fruit bat and the little brown bat are better masticatory models for *O. crassicaudatus* and early fossil primates. The dental and cranial morphology of these bats are more similar to those of the galago and the earliest primates than are those of modern humans. The same is true of masticatory behaviour.

The values for timing of peak activity are given in degrees of a 360 degree circle, where 0 degrees represents the point in the chewing cycle when centric occlusion ends and the teeth begin to separate. If one looks at the anterior camshaft from the right side, and the cams for the lateral pterygoids (0 degrees) are at the twelve o'clock position, then the cam for the working deep masseter (300 degrees) is at the two o'clock position and contacts its rocker arm *before* the lateral pterygoid does.

Blueprints for the all different kinds of cams were drawn by hand (Figure 6-3). The following describes the way I designed the cam for the working lateral pterygoid muscle (duration = 20% of the chewing cycle). First, I drew a circle, 5/16" in diameter, using a compass. Then I drew a line straight 'north' from the centre of the circle, continuing several inches beyond the top of the circle. Using a protractor, I then drew two lines. Each started at the centre of the circle, one northwest and one northeast, each making a 35 degree angle (i.e., 20% of a circle) with the north line. Then I marked a point 3/16" above the top of the circle on the north line, and I marked a point on each of the other two lines, 3/32" (i.e., one-half of 3/16) beyond the outline of the circle. Finally, I drew a curved line from the west side of the circle, up to the northwest point, crossing over the north point, down to the northeast point and finally joining the eastern edge of the circle. This curved line became the outline of the north half of the cam in side view (i.e., the 'high side'), whereas the south half of the circle remained unmodified and became the south half of the cam (or 'low side').

I cut out this egg-shape and traced it onto blocks of Plexiglas (in the case of the lateral pterygoids and the digastrics) or blocks of wood (for all other cams). I cut out the shapes using a band saw and an electric sander, then I drilled a 5/16" hole through the

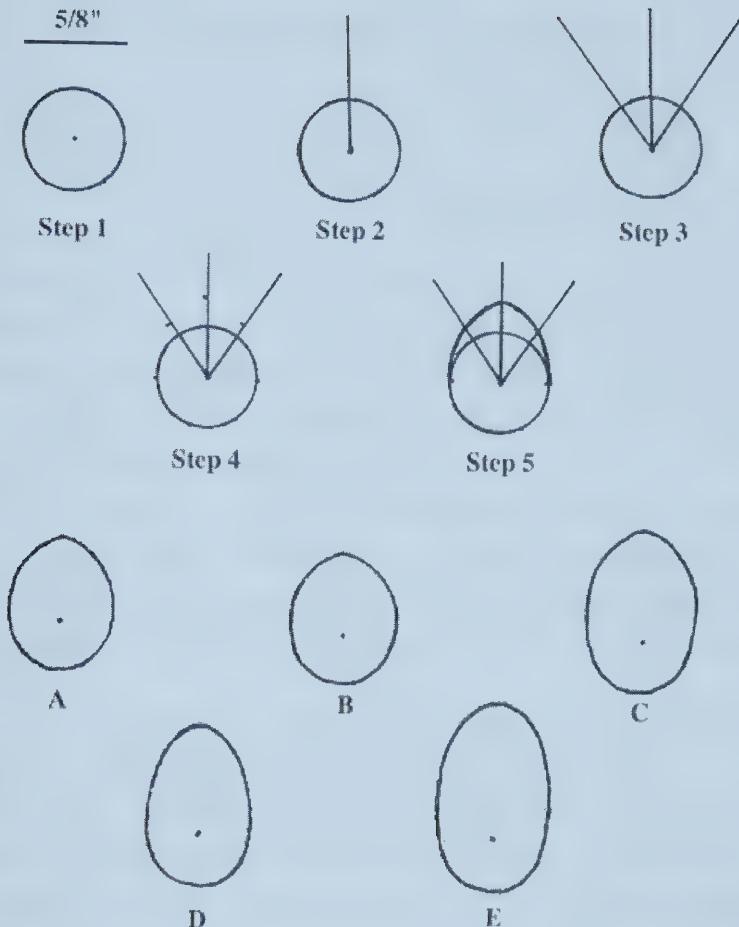


Figure 6-3 Cams. The five upper drawings detail the procedure used to generate the outline for the cam that activates the working lateral pterygoid muscle. The five lower drawings are the outlines used for the balancing lateral pterygoid (A), the digastrics (B), the medial pterygoids (C), the masseters (D) and the temporals (E). See text for description.

centre point of each. I glued one side of each cam onto the side of an aluminum sleeve (5/8" diameter, 5/16" bore), which I screwed onto the camshaft.

The cams for the balancing side lateral pterygoid, the working and the balancing side digastrics were designed similarly, but the angles used were 45 degrees, 60 degrees and 60 degrees respectively. The cams for the medial pterygoids were designed with a 45 degree angle also, but the height above the top of the circle is 3/8". This added height lends these cams added force. All other cams were designed using a 35 degree angle, but the height above the top of the circle for the masseters is 3/8", and that for the temporals is 9/16".

It proved necessary to melt paraffin wax onto the high sides of the largest wooden cams. This reduced the friction that threatened to set fire to my machine.

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Chapter 7: The experimental method

7.1 Theoretical considerations

It is important to draw the distinction between a hypothetical absolute diet and a hypothetical relative diet. The format of a hypothesis of absolute diet is as follows: *Plesiadapis rex* was a herbivore. Whereas a hypothesis about relative diet would follow this format: *Plesiadapis rex* was more herbivorous than *Pronothodectes matthewi*. Short of a time machine, there is no way to test a hypothesis about the absolute diets of most extinct primates.

The dental morphology of an extinct primate can, however, be compared to that of extant primates to infer the relative diet of the former. If *P. rex* has more dental characteristics in common with extant herbivorous primates than does *P. matthewi*, then it seems reasonable to infer that *P. rex* was more herbivorous than *P. matthewi*. Not only can this type of hypothesis be generated using comparative anatomy, but it can also result from experiments in functional morphology.

Using the machine, I have simulated mastication of fourteen kinds of food by 19 prosthetic tooth rows. Eleven tooth rows are specimens of extinct primates: six plesiadapiform species and five Eocene ‘true primates’. Five are specimens of extant primates, one is a specimen of *Tupaia glis*, and two are artificial. The aim of this experiment is to obtain data both qualitative and quantitative on how well each species breaks down each food. Performances can then be compared and species can be ranked as to their compatibility with different foods. Ultimately, species can be categorized tentatively as to ‘hypothetical relative diet’.

Of course, hypothetical relative diet is different from hypothetical absolute diet, and it is even further from true diet. There are several variables that contribute to an individual primate’s choice of a kind of food to eat. Physical properties of food are important contributing factors (Kinzey and Norconk, 1990), but primates also choose food based on availability (Overdorff, 1992) and nutritional quality (Sailer *et al.*, 1985) - factors that cannot be simulated mechanically. Ignorance of these factors can lead to erroneous conclusions. Ideally, studies of functional morphology do not consider only the physical properties of food. I omit the nutritional and distributional properties of food in my experiment, but they probably have little (or no) influence on tooth morphology.

The above reasons for choosing a particular food are *proximate*. *Ultimately*, if a certain kind of food cannot be broken down, the animal might break a tooth, hampering its future feeding success. It might be forced to abandon the food item, wasting the energy it

used to obtain it. Thus, selection favours a strong relationship between the form of the dentition (especially the premolars and molars) and the diet of the animal.

In cases of extraordinary preservation, the gut contents of a fossil mammal may be visible (Jepsen, 1966), and diet may be interpreted directly from the fossil. In other cases, small particles of plant material are trapped in the teeth and fossilize as phytoliths, as in the case of the fossil ape *Gigantopithecus* (Ciochon *et al.*, 1990).

The study of wear patterns and stable isotopes may be used to infer diet in extinct taxa. Results of these methods can be compared to results of experimental and morphometric methods.

To compare the masticatory performances of various prosthetic dentitions in a machine simulation, it is necessary to reduce the number of variables that can influence the measured performance. One can look at ‘the effectiveness of fragmentation’ as the dependent variable in this experiment. However, several variables related to simulated chewing might influence the dependent variable. The morphology (i.e., size and shape) of the molars and premolars is correlated to the effectiveness of fragmentation (e.g., Seligsohn, 1977). Therefore, I wanted to control all other variables, such that the variation in the dependent variable was solely influenced by variation in the size and shape of the premolars and molars. Because the sizes and shapes of these teeth are often the only determinants of species boundaries in early fossil primates, I am inadvertently measuring the influence of *taxonomic* variation on the effectiveness of fragmentation.

In order to isolate the influence of premolar and molar size and shape on effectiveness of fragmentation, it is necessary to control several variables. Some of the test specimens retained more than just p3-m3/P3-M3. These were cast, and the extra teeth were removed from the cast before it was installed in the machine. This was necessary because the presence of a canine in one specimen (of a species that retained the canine) might cause that specimen to outperform another specimen (of a species that also retained the canine) in which the canine is lost. Perhaps if both fossil specimens had retained the canine, they would have performed equally.

It was necessary to install all tooth rows in a similar position relative to the mandibular condyle. All tooth rows are 8 mm tall, from the base to the tip of the tallest tooth. Each lower tooth row was installed such that the posterior edge of the m3 was no more than 2 mm anterior to the anterior border of the ascending ramus of the mandible. I felt it best to hinge this measurement on the posterior edge of the m3 because the resultant vector of jaw muscle force during chewing always runs just posterior to the m3 in mammals (Greaves, 1995). Each upper tooth row was installed such that it occluded properly with the lower tooth row.

The action of the machine itself was also kept constant. Though it was necessary to reposition the cams and alter the jaw muscle forces (by loosening or tightening the eye bolts connected to the muscle cables) when I removed a tooth row from the right side and replaced it with one from the left side, or vice-versa.

Several studies of food-breakdown in humans measure how many times a subject has to chew a particular kind of food before he or she is prepared to swallow it. It would have been possible to do this in my experiment by measuring how many simulated chewing cycles were necessary to reduce an original food sample to particles of a given size. However, this would have been very time consuming, especially for very resistant kinds of food. Instead, I opted to keep the number of chewing cycles constant and I measured the resulting particle size distribution after ten chewing cycles. Most primates require more than ten chewing cycles before swallowing, even with soft foods (Hiiemae and Kay, 1973). The choice of ten chewing cycles (rather than five or 20) is somewhat arbitrary, though with this number of cycles, the machine can generate a measurable particle size distribution in a short period of time.

Each trial in my experiment consisted of a single sample of a particular kind of food that is chewed ten times by a particular dentition. With fourteen kinds of food, 19 different dentitions and five samples for each species-food pair, the main body of my experiment consisted of 1330 trials.

7.2 The procedure for an individual trial

In ‘recipe format’, the following is the procedure for a single trial:

- Wet the food sample¹ and pat it dry with a paper towel.
- Weigh the food sample using an electronic scale².
- Place the sample onto the lower tooth row³.
- Activate the machine and allow it to run for ten chewing cycles.
 - If the food sample falls off or broken pieces of it fall off, stop the machine and use forceps to place it back on the teeth. Restart the machine and allow it to complete the remaining cycles.

¹ Wetted food better approximates the condition of food in the mouth of a primate.

² The weight value displayed on the electronic scale tended to vary quite a bit for a few seconds before stabilizing. To compensate for this, I always waited 15 seconds before taking a measurement.

³ The geometric centre of the food sample was placed directly above the m2 talonid basin at the start of mastication, but food samples were usually displaced during mastication.

- Pass all the fragments through a column of four sieves and tap the sieves gently to allow fragments to settle. Avoid further breakage of the fragments inside the sieves.
- Recover all fragments from the first (i.e., coarsest) sieve.
- Calculate the mean of the longest axis and the shortest axis for each fragment⁴.
- Collect the fragments for which this value is greater than 5.6 mm, place them on weighing paper, and set them under a heat lamp until all visible water evaporates (usually about 15 seconds).
- Weigh the fragments.
- Collect the particles for which this value is less than 5.6 mm, place them on weighing paper, and set them under a heat lamp until all visible water evaporates.
- Weigh the fragments.
- Collect the particles from the next (finer) sieve, place them on weighing paper, and set them under a heat lamp until all visible water evaporates.
- Weigh the fragments.
- Repeat the last two steps for the final two sieves.

By following the above procedure, I could usually complete all the trials for one dentition (i.e., one set of tooth rows) in approximately ten hours.

7.3 Preparation of food prior to testing

The taxonomy of the animals and plants from which I obtained food for this study, and the reasons for selecting each food are detailed in Chapters 2 and 3 respectively.

Some of the foods I tested required very little preparation before testing them in the machine. Juniper berries (=cones, see Chapter 3), elderberries and barberries required no preparation. Other foods required substantial alteration. The purpose of these alterations was to approximate, as much as possible, the manual or incisal preparation that takes place before a primate is ready to put a food object in its mouth.

Rose petals, oak leaves and ginkgo leaves were cut into 1 cm x 1 cm sheets, then folded in half twice. This approximated the action of biting such a food down to a manageable size, then rolling it with the tongue to increase the height of the food item between the occlusal surfaces of the teeth. Special attention was paid to varying the location on the leaf/petal whence the 1 cm x 1 cm sheet was cut.

⁴ I was unable to obtain a sieve with a 5.6 mm aperture, so I used this method to approximate the action of such a sieve. It would have been easier to measure either the longest axis or the shortest axis, but that would produce erroneous results for oblong particles.

The wing was excised from each maple seed, leaving only the nutritionally rich portion for testing. The shells of the pistachios were removed and the remaining material

was cut into 1 cm x 0.5 cm x 0.5 cm chunks. Sumach fruits were detached from their leaves prior to testing.

Crickets and meal worms were sacrificed in 99% ethanol prior to testing, but were never stored in ethanol for more than a few days. This was not so much to simulate food preparation by primates, but rather to ease the testing procedure. It may be more realistic to test insects live; however, live crickets and meal worms make particularly unwilling test subjects. Furthermore, the ethanol did not noticeably affect the material properties of the insects during the short storage time.

Frozen chicken breast was thawed and cut into 1 cm x 0.5 cm x 0.5 cm chunks. Every effort was made to cut these chunks from areas lacking connective tissue. I also varied the long axis of the test chunk relative to the orientation of the muscle fibers.

Plums were also cut into 1 cm x 0.5 cm x 0.5 cm chunks. Each chunk was cut from the outside of the plum such that it had a layer of skin along one of its long sides.

The preparation of gum was extensive. I mixed gum arabic⁵ with water in a small container and poured it out into a shallow bowl. I added this mixture until the gum slurry in the bowl reached a thickness of 2-3 mm. After 24 hours of exposure to the air, the gum had usually become quite thick and had a rubbery consistency. I then cut the gum into 1 cm x 1 cm sheets. Prior to testing, I poured water onto the gum and allowed it to soak for half-an-hour until it had attained a toffee-like consistency. This approximates the consistency of Acacia exudates after they have been exposed and drying for several hours. Masticatory performance on highly fluid gum cannot be measured with respect to the size of chewed ‘fragments’.

7.4 Preparation of tooth rows prior to testing

The following is the typical procedure used for preparing a set of tooth rows prior to testing.

After casting a tooth row in methyl-methacrylate, all extraneous teeth and all non-dental parts of the mandible that project above the occlusal plane were sanded away. The proximal surface (i.e., where the tooth row attaches to the maxilla or mandible) of the tooth

⁵ This comes as a white powder that is often mixed with water to produce glue or icing.

row was sanded down to a flat surface, and then it was scratched shallowly but extensively using a dental pick. The resulting grooves provide added surface area for the bonding action of silicone without compromising the fit between the flat attachment surface of the maxilla/mandible and the attachment surface of the tooth row.

At least two hours prior to testing, I spread a thin layer of silicone sealant onto the attachment surface of the lower tooth row. I then cemented the tooth row to the mandible. This allowed the silicone plenty of time to set. The tooth row is likely to become detached from the mandible if the silicone is still wet by the time testing begins. With the lower tooth row in place (though the silicone need not be dry at this point), a layer of silicone was applied to the upper tooth row. With the aid of forceps, the upper tooth row was then negotiated into occlusal position. To cement the upper tooth row in place, it was usually necessary to adduct the lower jaw by hand and hold the teeth in occlusion for a few seconds.

After the silicone dried, I cleaned the occlusal surfaces. I then sprayed the occlusal surfaces with Pam cooking spray (mostly canola oil) to simulate the lubricating action of saliva⁶. After wiping away any excess oil with paper towel, I could begin the testing.

Note that if the tooth rows tested next were from the opposite side, considerable modification of the machine was necessary prior to testing. These modifications included swapping the cams from the left and right sides: working muscle cables became balancing muscle cables and vice versa. Also, corresponding muscles forces were switched by either tightening or loosening the eye bolt attached to each cable.

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⁶ I did this periodically throughout the testing procedure.

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Chapter 8: Results

8.1 Measures of fragmentation

There are several ways to interpret the results of an experiment like this one. Food items are broken down (or *triturated*) into fragments. These fragments constitute the raw data; therefore, any measurement of the effectiveness of trituration must depend on them.

Here I have kept the number, rate and strength of chews constant and I measured the resulting food fragments for different foods and different dentitions. Bates *et al.* (1976) refer to this as ‘masticatory performance’. This procedure can be rather messy though: small fragments may be lost if not monitored. Some studies on mastication in humans work the same way as this one. They have subjects chew a given food at a constant rate and intensity for a constant number of chews. Then they have the subject spit out the fragments, which are then measured (e.g., Yurkstas and Manly, 1950). Others keep the food fragment size constant (usually comfortable swallowing size). Then they record how many chews are necessary to achieve that fragment size. This procedure measures ‘masticatory efficiency’ (Bates *et al.*, 1976). Other studies examine the chewing strength necessary (e.g., Atkinson and Shepherd, 1967). Because there is no way for me to assess the ‘comfortable swallowing size’ of extinct primates, I kept everything else constant and measured the resulting particle size.

This type of assessment requires a few assumptions. The first assumption is that the most effective chewing performance is the one that causes the greatest increase in surface area for a given food volume. A greater surface area allows digestive enzymes greater access to molecules of food in the digestive tract, therefore minimizing digestion time for a given feeding bout (Chivers, 1982; Lambert, 1998). Here one must assume that animals (specifically primates) are *optimized* with respect to feeding behaviour and anatomy. That is, natural selection has acted on them to produce maximum efficiency in their functional anatomy. Most, if not all, biological structures are subject to many different selective forces. Therefore, morphology is often a compromise that responds to several selective forces; no structure is perfectly suited to the actions it performs.

However, given nearly constant environmental influences, natural selection works toward optimization over evolutionary time. For further discussion of this issue, see Chapter 4.

Given these assumptions, chewing effectiveness is measured here as the difference between the surface area to volume ratio *before* chewing and the surface area to volume ratio *after* chewing. Small spheres have more surface area (compared to volume) than do large spheres. Therefore, as an object is broken down (as in mastication, or more specifically trituration), the total resulting surface area increases with respect to the total resulting volume. The total volume of fragments after mastication is the same as the volume of the single food item prior to mastication, yet many more surfaces have now been exposed. The increase in surface area is easy to quantify when the initial food item and the final food fragments are all the same shape (e.g.. spheres). However, the resulting fragments are often different shapes, including rollers, blades, discs, etc.. Different shapes have different surface area to volume ratios – a fact that complicates data analysis. To accurately measure the surface area to volume ratio in a matrix composed of differently shaped fragments, one must measure surface area and volume directly from each particle. Because this was impracticable in this study (with more than 1500 matrices), I have chosen to assume that all fragments are spheres.

To calculate surface area, each sphere is assumed to have a diameter equal to the aperture size of the sieve in which it rests. The volume of a particle can be estimated by dividing its mass by its density¹. Food fragments were collected after mastication (see Chapter 7) and were passed through a column of sieves. Assuming all fragments in a sieve are the same size, one can estimate the volume of the individual fragments in a given sieve using density, total mass of all fragments in each sieve, and fragment radius ($=0.5 \times$ aperture size).

Inaccuracy occurs when 1. fragments in a single sieve are non-uniform with respect to size, 2. fragments are non-spherical, 3. the radius of a pre-chew particle is significantly larger than the aperture size of the largest sieve. Number 1 is especially problematic when there is a large difference in aperture size between a given sieve and the sieve above it; such a sieve would accumulate fragments of widely different sizes.

¹ I measured density by performing a water-displacement experiment for 5 samples of each kind of food.

Number 2 is especially problematic with certain foods (e.g., crickets) that tend to break into non-spherical fragments. 3. is a problem when the initial food item is necessarily large and variable from sample to sample. Crickets and meal worms are like this because I did not cut them down to a particular size. I felt it was more realistic to have the entire animal chewed.

I used the following formula to calculate the total volume of food fragments in a given sieve:

$$V_t = m / \rho \quad (8-1)$$

where V_t is volume in mm^3 , m is mass in g, and ρ is density in g/mm^3 .

Density is determined experimentally (water-displacement). Mass is measured by collecting all the food fragments from the sieve and weighing them.

I assumed all food fragments within a sieve are the same size and then I calculated the volume of an individual fragment within that sieve using,

$$V_1 = \pi r^3 4/3 \quad (8-2)$$

where V_1 is the volume of a single fragment and r is the aperture size of the sieve divided by two.

Equation 8-1 divided by equation 8-2 gives the number of fragments in a particular sieve ($=n$).

Next, I calculated the surface area to volume ratio of a spherical fragment for each of my five size categories. For each size category, I used the size of the aperture in the sieve as the diameter of the fragments that accumulate in the sieve. Thus, for the smallest size category, I used the aperture size of my smallest sieve: 0.5mm. I calculated the surface area to volume ratio by dividing the formula for the surface area of a sphere by the formula for the volume of a sphere, using the aperture size divided by two for the ‘radius’ value in each formula. The formula for the surface area of a sphere is

$$V = \pi r^2 4 \quad (8-3)$$

The formula for the volume of a sphere is

$$V = \pi r^3 4/3 \quad (8-4)$$

Therefore dividing 8-3 by 8-4 gives

$$3/r \quad (8-5)$$

As the radius of a particle gets smaller, the value for 8-5 gets bigger. For the coarsest sieve, the value for 8-5 is about 1.07 (3 / 2.8mm); for the finest sieve, it is 12 (3 / 0.25mm). Given the above assumptions, a good measure of the effectiveness of fragmentation for a particular size category is given by the number (n) of fragments in that size category multiplied by the value for 8-5 for that size category. Thus,

$$\omega = 3n / r \quad (8-6)$$

where ω is the surface area to volume ratio for a given size category, n is the number of fragments in that size category and r is the size of the apertures of the sieve that holds all the fragments.

The values of ω for the five size categories are added together. This sum is then deducted from the ω value for the initial food item (assuming the initial food item has a diameter equal to the aperture size of the coarsest sieve). The difference is the ' Ω^2 value' (masticatory performance or effectiveness of fragmentation). The Ω values for different species and for different foods can be compared to assess differential masticatory performance among them.

Some kinds of food may be easier to break than others. Perhaps some dentitions are universally more effective at breaking food than are others. I attempted to compensate for these two biases in my results. To do so, I calculated the mean Ω value for each kind of food and for each species. I then determined the percent difference between each Ω value and the mean Ω value for that food, using the following formula:

$$\Omega_{\text{food}} = 100((\Omega_x - \Omega_{\text{mean}}) / \Omega_{\text{mean}}) \quad (8-7)$$

where Ω_x is the effectiveness of fragmentation for a single species-food pair, Ω_{mean} is the mean effectiveness of fragmentation for a given kind of food, and Ω_{food} is the food-averaged effectiveness of fragmentation for that species-food pair.

The same operation is performed using the mean Ω value for a given species. This gives a Ω_{species} value. The Ω_{species} and the Ω_{food} are then averaged to get the doubly averaged Ω value (once by food and once by species). Converting initial Ω values into doubly averaged Ω values partly compensates for the differential resistance of different kinds of food to deformation, and the differential effectiveness of different dentitions.

² This use of the Greek letter omega is purely arbitrary.

Results presented here are either raw or doubly averaged Ω values. For example, to assess whether or not there is a correlation between effectiveness of fragmentation and a particular tooth measurement (see Chapter 4), I used the *doubly averaged* Ω values. Raw and doubly averaged Ω values for all species and kinds of food are presented in tabular format in Appendix 2. Only those values of particular interest are presented in this chapter.

For simplicity, I often refer to the general food groups, rather than specific kinds of food. A value for ‘insects’ is simply the mean of the corresponding values for crickets and meal worms. Specific foods are grouped into general categories not on true anatomical grounds, but rather on similarities in structural properties. This is justified for a study of functional morphology (Yamashita, 1996).

8.2 Effectiveness of fragmentation

Figure 8-1 is a histogram that shows the effectiveness of fragmentation for the four major groups of test dentitions given six general categories of food.

As the values in Figure 8-1 are doubly averaged, the differences among the poorer performances are exaggerated. This facilitates analysis of relative performances; however, it exaggerates the difference in performance between groups. Hence, the very different pattern between plesiadapiforms and euprimates shown here does not necessarily reflect a major dietary difference between these two groups. Rather, this question is addressed below.

To determine whether or not the differences shown in Figure 8-1 are significant, I compared the plesiadapiform mean performance to the euprimate mean performance for each general category of food. I made the same comparison between plesiadapiforms tested and extant primates tested, as well as between the euprimates and the extant primates. Differences between means were assessed using a normal probability distribution to see whether the differences were significant or not. Significance was judged at the 10% level (p value = 0.10). Raw Ω values were used in this test. For this test, I followed the standard procedure for comparing the means of two large samples (e.g., Bailey, 1997, pp. 40-43).

Table 8-1 shows the results of this test of significance. There is a significant difference between the mean Ω values of the major primate groups examined here. The difference between the plesiadapiforms and the Eocene euprimates is also much smaller than the difference between plesiadapiforms and extant primates and the difference between Eocene euprimates and extant primates. This indicates that plesiadapiforms and Eocene euprimates are similar with respect to the fragmentation of food. Eocene euprimates are relatively similar to extant primates, though less so.

Plesiadapiforms fragmented herbaceous foods, gum and meat significantly better than did Eocene euprimates. However, they fragmented insects much worse. Extant primates proved better than plesiadapiforms at fragmenting all foods, especially insects. Though for herbaceous foods, nuts/seeds and gum, the difference is insignificant at the 10% level. Extant primates performed significantly better than Eocene primates on all foods except fruit.

Compared to the other groups, Eocene euprimates performed very well on fruit. Plesiadapiformes did well with leaves and flower petals and gum, whereas extant primates fragmented insects and meat very effectively. These masticatory performances partly reflect the individual species chosen. For example, most of the extant species in this study are known to be insectivorous. The results in Table 8-1 do not suggest that extant primates are generally more insectivorous than plesiadapiforms. Rather, the extant taxa *in this study* are more insectivorous than the plesiadapiforms *in this study*. In this context it is noteworthy that the extant taxa fragmented all foods except fruit more effectively than did their extinct counterparts.

At the family level, several differences exist with respect to the effectiveness of fragmentation. Results are shown in Figure 8-2. Among extinct taxa, plesiadapids fragmented fruit, nuts and seeds very well. Carpolestids were generally very proficient ‘tritulators’ especially when given nuts, seeds or gum. Paromomyids and palaechthonids exhibited a similar pattern, specializing on nuts and seeds and, to a lesser degree, fruit. Notharctids performed somewhat like plesiadapids and somewhat like omomyids. They demonstrated talent for fragmenting fruit, nuts and seeds. Omomyids performed well on fruit and insects.

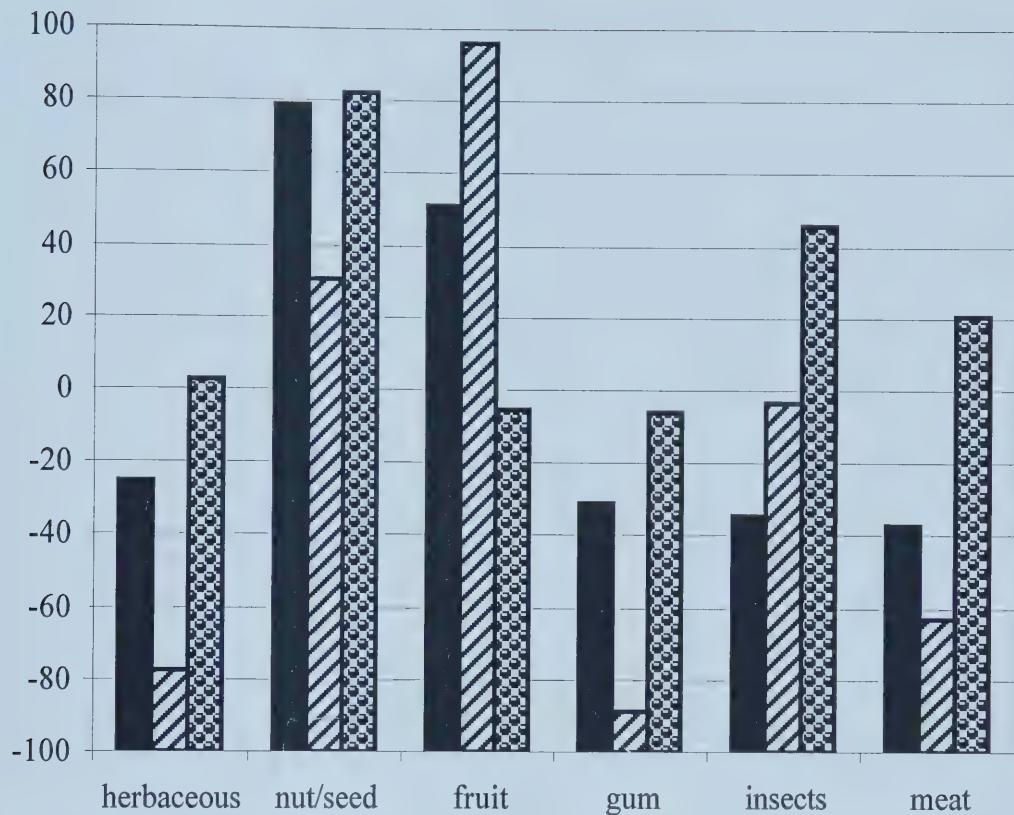


Figure 8-1 Effectiveness of fragmentation: large groups. Doubly averaged Ω values are on the y-axis. Solid black bars represent plesiadapiforms (*Plesiadapis churchilli*, *Plesiadapis fordinatus*, *Carpodaptes hazelae*, *Carpolestes dubius*, *Phenacolemur praecox* and *Plesiolestes problematicus*). Hatched bars represent euprimates (*Cantius eppsi*, *Notharctus sp.*, *Smilodectes gracilis*, *Tetonius matthewi* and *Arapahovius gazini*). Bubbled bars represent extant taxa (*Lemur catta*, *Otolemur crassicaudatus*, *Loris tardigradus*, *Nycticebus coucang*, *Tarsius spectrum* and *Tupaia glis*). ‘Herbaceous’ foods are rose petals, oak leaves and ginkgo leaves. ‘Nut/seed’ includes maple seeds, sumach fruits and pistachios. ‘Fruit’ includes juniper ‘berries’, barberries, elderberries and plum. ‘Gum’ is gum arabic. ‘Insects’ includes crickets and meal worms. ‘Meat’ is raw chicken breast.

food	Major group 1	group 2	n1	n2	d	p	confidence limits	min	max
Herbaceous nut/seed	Plesiadapiforms	Euprimates	90	75	5.06	<0.001	0.034	0.078	
	Plesiadapiforms	Euprimates	90	75	1.83	0.10	-0.011	0.335	
	Gum	Plesiadapiforms	30	25	2.83	0.01	0.009	0.047	
	Insects	Plesiadapiforms	60	50	-3.79	<0.001	0.026	0.083	
	Meat	Plesiadapiforms	30	25	2.09	0.05	0.002	0.072	
	Fruit	Plesiadapiforms	120	100	-1.05	insignificant	-0.055	0.180	
				mean	2.78				
Herbaceous nut/seed	Plesiadapiforms	Extant	90	90	-0.85	insignificant	-0.031	0.078	
	Plesiadapiforms	Extant	90	90	-0.96	insignificant	-0.097	0.284	
	Gum	Plesiadapiforms	30	30	-0.93	insignificant	-0.013	0.037	
	Insects	Plesiadapiforms	60	60	-13.16	<0.001	0.186	0.251	
	Meat	Plesiadapiforms	30	30	-2.40	0.02	0.016	0.156	
	Fruit	Plesiadapiforms	120	120	2.53	0.02	0.022	0.173	
				mean	3.47				
Herbaceous nut/seed	Extant	Euprimates	90	75	3.00	0.01	0.028	0.131	
	Extant	Euprimates	90	75	2.88	0.01	0.081	0.429	
	Gum	Euprimates	30	25	4.50	<0.001	0.023	0.057	
	Insects	Euprimates	60	50	2.64	0.01	0.042	0.286	
	Meat	Euprimates	30	25	3.41	<0.001	0.052	0.194	
	Fruit	Euprimates	120	100	-2.76	0.01	0.047	0.275	
				mean	3.20				

Table 8-1 Results of a significance test that compares raw Ω values of major groups.

'n1' and 'n2' are the sample size for major taxonomic group 1 and 2 respectively. 'd.' is the test statistic. It is a ratio: the mean of group 1 minus the mean of group 2 divided by the square root of ((estimated variance of group 1 / n1) + (estimated variance of group 2 / n2)). 'p' indicates at what percent level d is significant. A judgment of 'insignificant' means that d is insignificant at the 10% level ($p > 10\%$). If d is positive, then group 1 is significantly better at fragmenting the food listed; if it is negative, then group 2 is better. The mean d is calculated using absolute values of d. In this sample, the difference between the mean performance of group 1 and the mean performance of group 2 will fall between the minimum and maximum confidence limits with a 95% probability.

Family level comparisons for extant taxa are unnecessary because all but two species (*N. coucang* and *L. tardigradus*) are in separate families. Therefore, I compared extant taxa at the species level. Results are presented in Figure 8-3. *O. crassicaudatus* demonstrated proficiency for most food categories. It did particularly well when given nuts, seeds, herbs and gum. Its high score for herbaceous foods relies almost entirely on a high score for rose petals – it does very poorly with leaves. *L. tardigradus* did well with meat and insects. *T. glis* also did well with insects, though it also fragmented nuts, seeds and gum reasonably well. *N. coucang* did reasonably well with several foods, though it excelled with none. It fragmented nuts, seeds, fruit and insects best. *T. spectrum* showed a similar pattern to that of *N. coucang*, though it performed better when

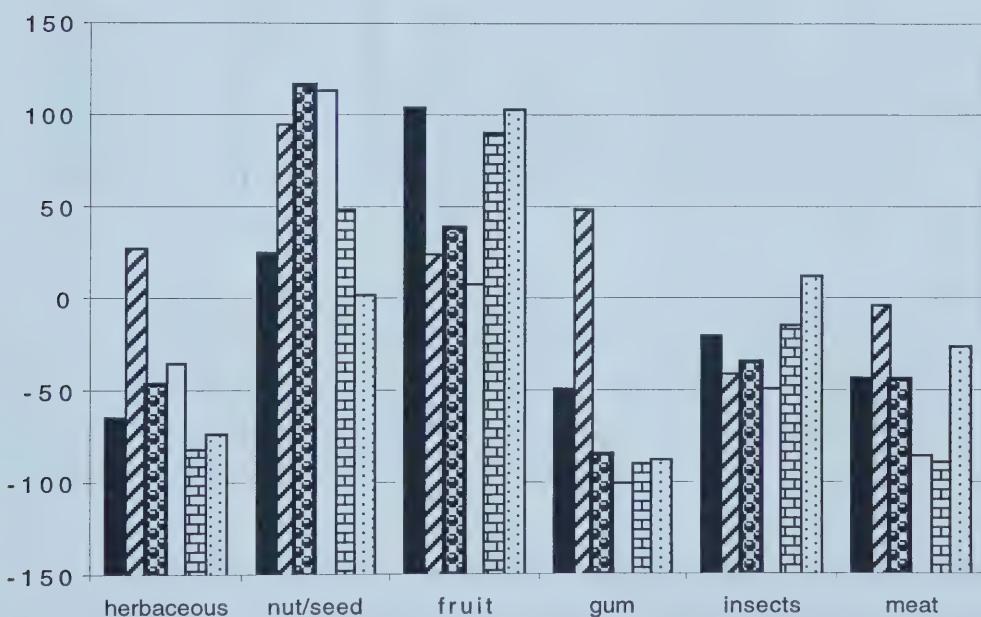


Figure 8-2 Effectiveness of fragmentation: families. As for Figure 8-1. Black bars represent plesiadapids, hatched bars represent carpolestids, bubbled bars represent paromomyids, white bars represent palaechthonids, bricked bars represent notharctids and spotted bars represent omomyids.

given meat. *Lemur catta* did well with nuts, seeds, herbs and gum. *L. catta*'s high score for herbs relies almost entirely on its high score for leaves (ginkgo and oak); its performance on rose petals was poor.

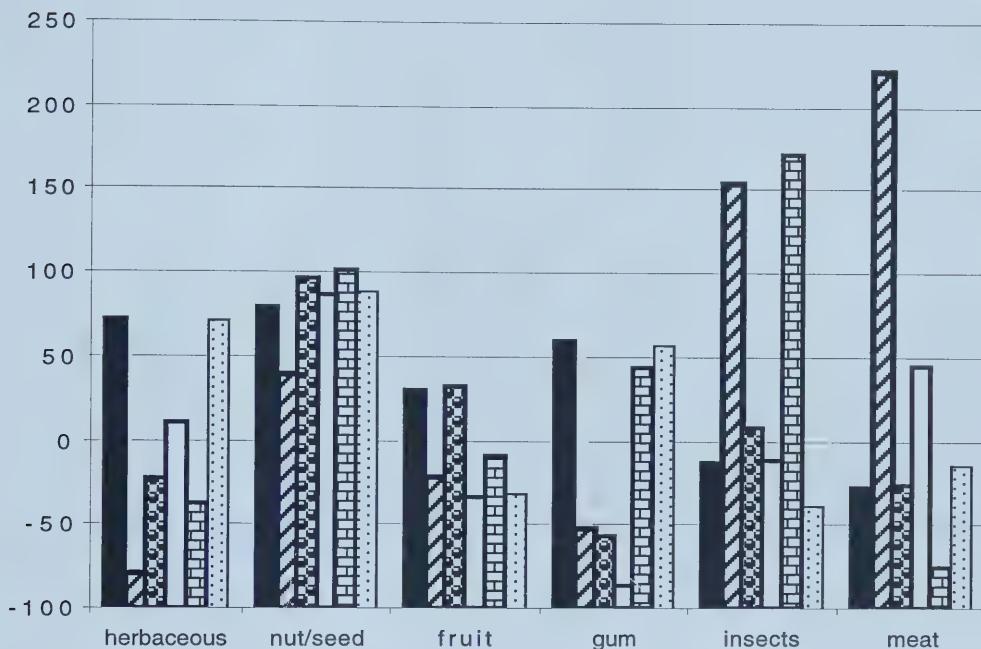


Figure 8-3 Effectiveness of fragmentation: extant species. As for Figure 8-1. Black bars represent *O. crassicaudatus*, hatched bars represent *L. tardigradus*, bubbled bars represent *N. coucang*, white bars represent *T. spectrum*, bricked bars represent *T. glis* and spotted bars represent *L. catta*.

Values for the effectiveness of fragmentation by plesiadapiform species are given in Figure 8-4. *Plesiadapis* species performed similarly. Both emphasized nuts and fruits; *P. churchilli* fragmented fruits considerably better, but *P. fordinatus* performed better on everything else. The carpolestids showed greater variation. They both emphasized plant material, but *Carpolestes dubius* outperformed *Carpodaptes hazelae* when fragmenting flowers, leaves, nuts and seeds. The latter vastly exceeded all other species' performances on gum. Relative to other plesiadapiforms, it also performed well on meat.

Carpodaptes dubius displayed some ability to fragment gum, exceeding all other plesiadapiforms except *C. hazelae*. Despite being in different families, *P. praecox* and

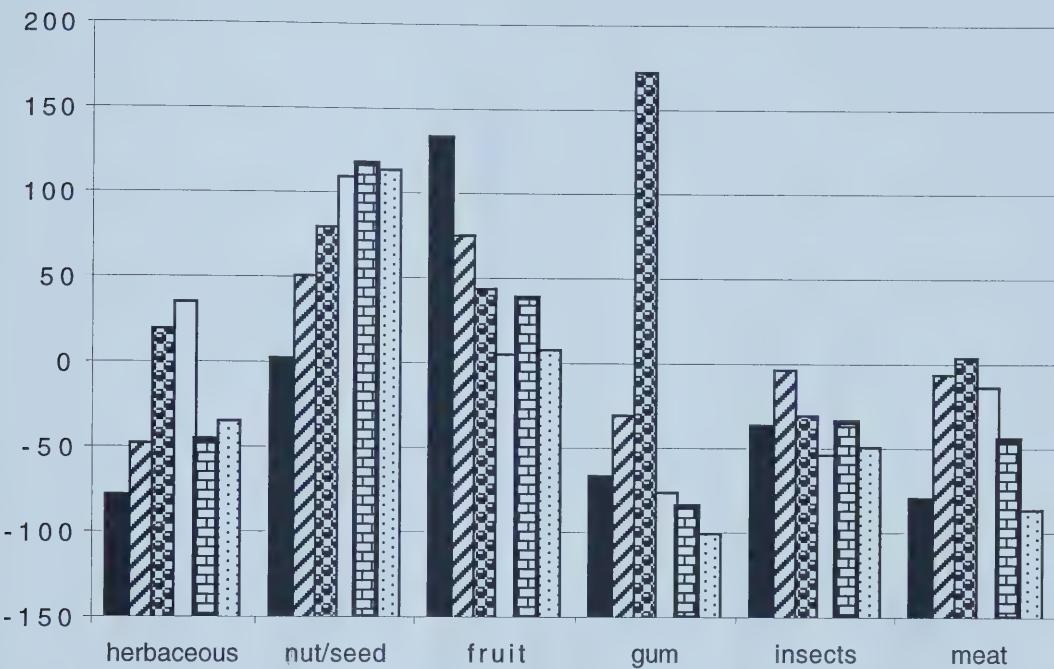


Figure 8-4 Effectiveness of fragmentation: plesiadapiform species. As for Figure 8-1. Black bars represent *Plesiadapis churchilli*, hatched bars represent *P. fodinatus*, bubbled bars represent *Carpodaptes hazelae*, white bars represent *Carpolestes dubius*, bricked bars represent *Phenacolemur praecox* and spotted bars represent *Plesiolestes problematicus*.

P. problematicus fragmented test foods with similar effectiveness. They both did very well with nuts and seeds, and moderately well with fruit.

Striking patterns are revealed by the results for the Eocene euprimates (Figure 8-5). Species belonging to the same family do not show similar patterns. *Cantius eppsi* (Adapidae) performed similarly to *Notharctus sp.* (Adapidae), but the latter did much better with insects. *Notharctus sp.* also performed similarly to *Arapahovius gazini* (Omomyidae). Conversely, *A. gazini* did very well with meat and *Notharctus sp.* did not. *Cantius eppsi* did very well with nuts and seeds and little else. *Notharctus sp.*

fragmented nuts, seeds and insects effectively. *Arapahovius gazini* did well with insects and does moderately well with nuts and seeds. Though *Smilodectes gracilis* is an adapid

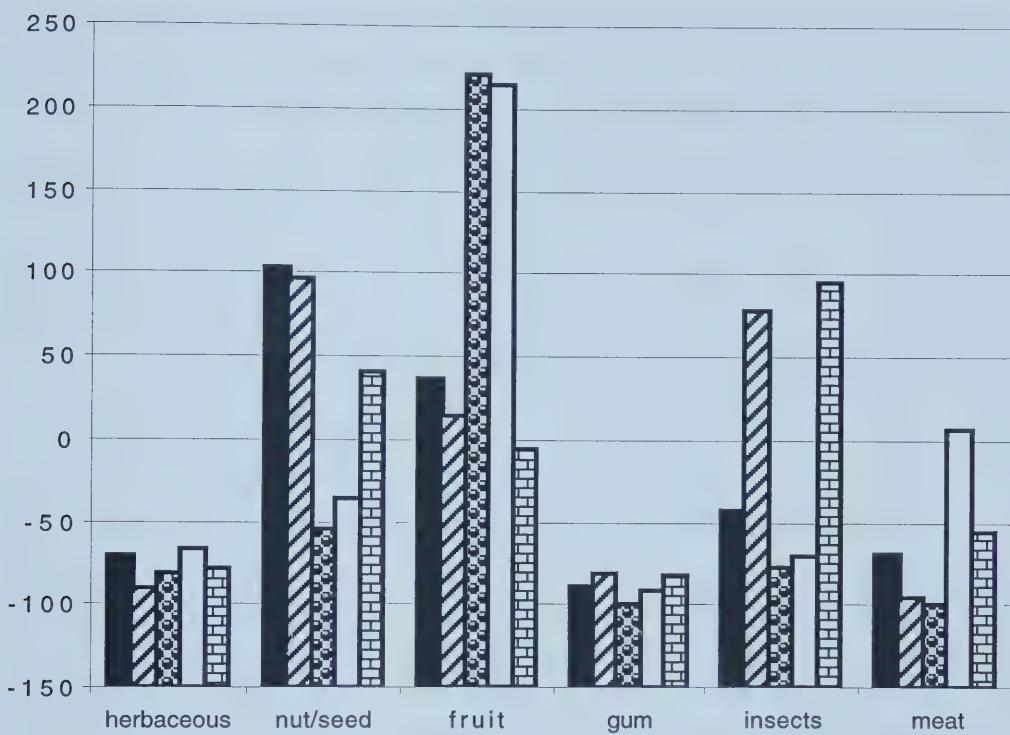


Figure 8-5 Effectiveness of fragmentation: Eocene euprimate species. As for Figure 8-1. Black bars represent *Cantius eppsi*, hatched bars represent *Notharctus sp.*, bubbled bars represent *Smilodectes gracilis*, white bars represent *Tetonius matthewi* and bricked bars represent *Arapahovius gazini*.

and *Tetonius matthewi* is an omomyid, they fragmented food with comparable effectiveness. *S. gracilis* fragmented fruit exceedingly well, but did a poor job with everything else. *T. matthewi* also fragmented fruit exceedingly well, but also did well with meat.

To assess whether or not there are significant differences in fragmentation performances, I first compared performances to see which species was most successful and which was least successful in breaking up the various foods. The maximum and

minimum performers for each specific and each general food category are shown in Table 8-2.

Exceptional performances, both positive and negative, were noted and chosen for a second round of chewing tests. The purpose of this second round of testing was to see whether certain species would perform consistently poorly given certain foods, or

food	Maximum: raw score		Minimum: raw score		Maximum: doubly averaged		Minimum: doubly averaged	
barberry	7.73E-01	O.c.	1.55E-02	Noth.	184.38	O.c.	-93.86	Noth.
chicken	4.85E-01	L.t.	-2.49E-05	S.g	222.82	L.t.	-100.02	S.g.
cricket	9.81E-01	L.t.	3.11E-02	S.g	225.25	L.t.	-86.04	S.g.
elderberry	1.32E+00	T.m.	1.61E-01	Pl. p.	341.33	S.g.	-48.28	C.d.
ginkgo leaf	2.14E-01	L.c.	-2.60E-05	S.g.	114.49	L.c.	-100.03	S.g.
gum arabic	1.33E-01	C.h	-1.30E-05	Pl. p.	169.00	C.h.	-100.03	Pl.p.
juniper	6.05E-01	C.h	1.93E-05	Pointy	116.28	A.g.	-99.99	Pointy
larva	4.53E-01	Noth.	-1.25E-05	Pointy	131.49	Noth.	-100.01	Pointy
maple seed	5.52E-01	T.g.	-1.82E-04	S.g.	155.38	T.g.	-100.11	S.g.
oak leaf	1.85E-01	L.c.	-1.49E-05	N.c.	161.26	L.c.	-100.02	N.c.
pistachio	1.65E+00	Ph. p.	2.45E-01	T.m.	283.06	Pl.p.	-48.15	T.m.
plum	1.48E+00	T.m.	8.82E-02	O.c.	312.63	T.m.	-76.09	O.c.
rose petals	4.90E-01	O.c.	-2.95E-05	Noth.	287.97	O.c.	-100.02	Noth.
sumach	1.81E-01	C.h	8.65E-03	S.g.	19.91	C.e.	-93.56	S.g.
herbaceous	1.71E-01	O.c.	8.85E-03	Noth.	72.54	L.c.	-90.77	Noth.
nut/seed	7.69E-01	T.g.	8.47E-02	S.g.	116.75	Ph.p.	-54.15	S.g.
gum	1.33E-01	C.h	-1.30E-05	Pl. p.	220.91	S.g.	-33.73	T.s.
insects	7.05E-01	L.t	1.64E-02	Pointy	173.23	C.h.	-100.03	Pl.p.
meat	4.85E-01	L.t	-2.49E-05	S.g.	171.78	T.g.	-85.46	Pointy
fruit	8.22E-01	T.m.	1.65E-01	T.s.	221.74	L.t.	-100.02	S.g.

Table 8-2 Maximum and minimum performers for all food categories. Species abbreviations are given in Appendix 1. Raw scores are raw Ω values; doubly averaged scores are doubly averaged Ω values; that is Ω values scaled to both the mean for a particular food and the mean for a particular species. For example, 7.73E-01 in the first column is scaled to the mean value for barberries and to the mean value for *O. crassicaudatus*, to get 184.38 (in the third column).

whether a new round of testing would produce completely different results. The latter would suggest that there are inconsistencies in the method used here.

I replicated the chewing experiment using two dentitions for each kind of food. For instance, I tested gum again, using *Carpodaptes hazelae* (the best fragmenter of gum) and *Plesiolestes problematicus* (the worst). This time, I used ten samples per species rather than five. This replicate test consisted of 280 trials; the results are shown in

Appendix 3. I compared the *original* mean masticatory performance of a given species-food pair to the mean for the corresponding *replicate* test. To do so, I used the standard procedure for comparing the means of two small samples (Bailey, 1997, pp. 55-58). The results of this analysis are shown in Table 8-3.

food	species	n2	n1	d	p	min	max
barberries	<i>O. crassicaudatus</i>	10	5	0.499	insignificant	-0.977	1.431
barberries	Pointy	10	5	0.010	insignificant	-1.043	1.051
chicken	<i>L. tardigradus</i>	10	5	0.912	insignificant	-0.812	1.667
chicken	<i>S. gracilis</i>	10	5	-0.005	insignificant	-1.044	1.041
crickets	<i>S. gracilis</i>	10	5	0.103	insignificant	-1.029	1.112
crickets	<i>T. glis</i>	10	5	0.693	insignificant	-0.943	1.612
elderberries	<i>P. problematicus</i>	10	5	0.540	insignificant	-0.944	1.429
elderberries	<i>T. matthewi</i>	10	5	1.180	insignificant	-0.660	1.721
ginkgo leaves	<i>C. dubius</i>	10	5	0.390	insignificant	-0.979	1.318
ginkgo leaves	<i>S. gracilis</i>	10	5	0.000	insignificant	-1.044	1.044
gum arabic	<i>C. hazelae</i>	10	5	0.052	insignificant	-4.814	5.008
gum arabic	<i>P. problematicus</i>	10	5	0.002	insignificant	-1.043	1.045
juniper	<i>C. hazelae</i>	10	5	0.946	insignificant	-0.805	1.700
juniper	Pointy	10	5	-0.002	insignificant	-1.044	1.043
maple seeds	<i>S. gracilis</i>	10	5	0.131	insignificant	-1.024	1.130
maple seeds	<i>T. glis</i>	10	5	2.513	0.05	-0.043	1.697
meal worms	<i>L. tardigradus</i>	10	5	0.905	insignificant	-0.842	1.718
meal worms	Pointy	10	5	0.132	insignificant	-1.023	1.131
oak leaves	<i>N. coucang</i>	10	5	0.094	insignificant	-1.029	1.105
oak leaves	<i>T. glis</i>	10	5	0.139	insignificant	-1.023	1.137
pistachios	<i>Ph. praecox</i>	10	5	1.122	insignificant	-2.131	5.269
pistachios	<i>S. gracilis</i>	10	5	16.393	<0.001	0.779	1.078
plum	<i>O. crassicaudatus</i>	10	5	0.120	insignificant	-1.027	1.124
plum	<i>T. matthewi</i>	10	5	1.276	insignificant	-0.640	1.834
rose petals	<i>Notharctus</i> sp.	10	5	-0.011	insignificant	-1.045	1.037
rose petals	<i>O. crassicaudatus</i>	10	5	0.086	insignificant	-1.216	1.298
sumachs	<i>C. eppsi</i>	10	5	0.249	insignificant	-1.006	1.215
sumachs	<i>S. gracilis</i>	10	5	0.088	insignificant	-1.030	1.102

Table 8-3 Results of a significance test that compares original means with replicate means. ‘n1’ and ‘n2’ are the sample size for the original test and the replicate test respectively. As for Table 8-1, ‘d’ is test statistic and ‘p’ indicates at what percent level d is significant. A judgment of ‘insignificant’ means that the d is insignificant at the 10% level ($p > 10\%$). If d is positive, then that species did better in replicate testing than it did originally. The difference in means will fall between the minimum and maximum confidence limits with a 95% probability.

Raw Ω values were used in this test.

Of the 28 replicate tests I performed, only two yielded results that were significantly different from the original results. Few significant differences suggests that species (i.e., dentitions) perform similarly in different instances; therefore, the method used here is consistent. *Smilodectes gracilis* did significantly better with pistachios in the repeated test ($p < 0.1\%$), and *Tupaia glis* did significantly better ($p = 5\%$) with maple seeds. Of the species tested, *T. glis* was already the best fragmenter of maple seeds; therefore, this difference does not have an impact on the ranking of species with respect to food category. The rank of *S. gracilis* for pistachios, and for nuts and seeds in general, would be improved substantially with the incorporation of the replicate data. However, any benefits of this inclusion are outweighed by the costs of changing my experimental method and testing all species-food pairs again. For the remainder of my statistical analyses, I used only the data from my original tests. Many analyses were performed using raw Ω values (rather than doubly averaged ones). However, doubly averaged values were used in graphical analyses and displays (e.g., tests of correlation) because they allow for visual distinctions among poor performances.

Does my experimental method actually generate significantly different fragmentation performances by different species? To answer this question, I compared the fragmentation performance mean of the best fragmenter of fruits to that of the worst fragmenter of fruits. Using the standard method for comparing the means of two small samples (as above), I repeated this comparison for all six general categories of food. Instead of testing whether the means are significantly *different*, I tested whether or not the mean for the better performance is significantly *better* than the other. In all cases, the higher mean was *significantly* higher (see Table 8-4). However, the mean value for *O. crassicaudatus* given herbaceous foods was only significantly higher than that of *Notharctus sp.* at the 25% level. Notwithstanding, a significant difference for most foods suggests that my experimental method generates significant results.

I performed the same significance test for each specific food category. In thirteen out of fourteen cases, the most ‘adept’ species scored significantly higher (at the 5% level or better) than the most ‘inept’ species. The single exception was rose petals. This suggests that the lack of significant differences among tests on rose petals is the source of the high p-value for herbaceous foods (above, see Table 8-4). Differences among oak

food	Adept	Inept	n1	n2	d	p	min	max
herbaceous	O.c.	Noth.	15	15	1.068	<0.05%	-0.096	0.420
nut/seed	T.g.	S.g.	15	15	3.807	<0.05%	0.379	0.990
gum	C.h	Pl. p.	5	5	5.532	<0.05%	0.088	0.178
insects	T.g.	Pointy	10	10	3.750	<0.05%	0.370	1.007
meat	L.t	S.g.	5	5	4.565	<0.05%	0.288	0.683
fruit	T.m.	T.s.	20	20	4.090	<0.05%	0.386	0.928

Table 8-4 Results of a significance test that compares the best and worst performances for a given category of food. ‘n1’ and ‘n2’ are the sample size for the best performer (‘adept’) and the worst (‘inept’) respectively. As for Table 8-1, ‘d’ is the test statistic and ‘p’ indicates at what percent level d is significant. The difference in means will fall between the minimum and maximum confidence limits with a 95% probability. Raw Ω values were used in this test. The meanings of abbreviations for species names are given in Appendix 1.

leaves and among ginkgo leaves were extremely significant ($p < 0.05\%$).

For each general food category, I ordered species from the most effective fragmenter to the least effective. Then I tested them to see if species A performed significantly better than the *next* most effective species. A comparison of the means of two small samples was used to test significance. Most differences were insignificant. Thus, for each general food category, the species tested represent a continuum from the most effective fragmenter, down to the least effective fragmenter. Few significant gaps exist in this continuum. This makes it very difficult to draw a distinction between those species adept at fragmenting insects, for example, from those species *inept* at fragmenting insects. There are few exceptions. One is the performance of *Loris tardigradus* on meat compared to the next best performance on meat, that of *Tarsius spectrum*. *L. tardigradus* does significantly better with meat ($p = 2.5\%$) than does *T. spectrum*. Also, *Carpodaptes hazelae* does significantly better with gum than does its closest contender, *Otolemur crassicaudatus*, though this difference is only significant at the 10% level.

I then plotted raw Ω values for all species in six histograms, one for each general category of food. Species were ordered from left to right based on decreasing raw Ω values. I noted the adjoining pair of species that had the greatest difference in raw Ω value. Based on this difference, I divided species into two categories for each food: adept fragmenters and inept fragmenters. For example, the greatest difference between

adjoining pairs for herbaceous foods was between *Lemur catta* and *Carpolestes dubius*. The most effective fragmenter of herbaceous foods is *Otolemur crassicaudatus*. *Lemur catta* is next, followed by *Carpolestes dubius*. All other species performed more poorly on herbaceous foods. I divided species into herbaceous-adepts (*O. crassicaudatus* and *L. catta*) and herbaceous-inepts (*C. dubius* and all other species). I then took the mean for all herbaceous-adepts and compared it to the mean for all herbaceous-inepts. Finally, I performed a significance test (either comparison of means of small or of large samples, one-tailed test) to examine whether or not adepts performed significantly better than inepts. I then repeated this procedure for the next greatest difference between adjoining species to determine which species were somewhat adept.

For all general food categories, with the exception of herbaceous foods, the adept group did significantly better than the inept group ($p < 0.05\%$). At the 5% level, the difference between herbaceous-adepts and herbaceous-inepts was insignificant. Table 8-5 lists the adept, somewhat adept and inept species for each general food category. It is important to note that these distinctions are drawn at *gaps* between performance scores. If a sample of several different species were scored with respect to ‘degree of carnivory’, one might be able to separate ‘true carnivores’ from ‘non carnivores’ based on large differences in degree of carnivory. This would be relatively easy for a sample consisting of a dog, a cat, a ferret, a cow and a deer. However, when the disparity in the degree of carnivory is minimal (i.e., gaps are all about the same size), it is very hard to separate species into such discrete categories. The same is true here. If the taxa in this study are to be separated into dietary categories based on the results of the food fragmentation experiment, then gaps in performance must be analyzed.

I performed a similar analysis on the effectiveness of fragmenting specific foods. I tested the significance for only five specific categories, but the differences for each of these five were highly significant ($p < 0.05\%$). Table 8-6 lists adept, somewhat adept and inept species for each specific kind of food.

	Adept	Somewhat adept	Inept
herbaceous	<i>Otolemur crassicaudatus</i> <i>Lemur catta</i>	<i>Tarsius spectrum</i> <i>Carpodaptes hazelae</i> <i>Carpolestes dubius</i>	All other species
nut/seed	<i>Tupaia glis</i> <i>Phenacolemur praecox</i>	All other species	<i>Plesiadapis churchilli</i> Pointy <i>Tetonius matthewi</i> <i>Smilodectes gracilis</i>
gum	<i>Carpodaptes hazelae</i>	<i>Otolemur crassicaudatus</i> <i>Lemur catta</i> <i>Tupaia glis</i>	All other species
insects	<i>Tupaia glis</i> <i>Loris tardigradus</i>	<i>Notharctus</i> sp. <i>Arapahovius gazini</i>	All other species
meat	<i>Loris tardigradus</i>	<i>Tarsius spectrum</i>	All other species
fruit	<i>Tetonius matthewi</i>	<i>Smilodectes gracilis</i>	All other species

Table 8-5 Tentative dietary inferences based on analysis of gaps in raw Ω values: general categories of food. See text for a description of the method used to determine adeptness. Species are listed in order of descending raw Ω values.

8.3 Fragmentation results and morphometric results compared

8.3.1 Parametric methods

To assess how well different morphometric methods predict food breakdown, I compared the results of my morphometric studies to those of the food fragmentation experiment. This assumes that predictions made from the mastication experiment are correct. Morphometric methods were applied to the same specimens used in the experiment, therefore dietary predictions made based on those specimens should apply to experimental performances. Artificial dentitions (Flat and Pointy) were omitted from this analysis because it was impossible to apply the morphometric methods to them.

To assess the correlation between results of Seligsohn's method and experimental performances, I plotted the mean of six (out of seven) Seligsohn indices (see Chapter 4) against experimental performances. These indices measure the degree of insectivory (versus frugivory) of test dentitions. I used the doubly averaged Ω values and general

	Adept	Somewhat adept	Inept
barberry	O. c.	S. g., P. c., P.f., C.e., Flat, C.h.	All other species
chicken	L. t.	T. s.	All other species
cricket	L. t., T.g.	A. g.	All other species
elderberry	T. m., S.g.		All other species
ginkgo leaf	L.c., C.d., T.s., N.c.	P.f., Flat, T.g., Pl.p., C.h., Ph.p	All other species
gum arabic	C.h.	O.c., L.c., T.g.	All other species
juniper	C.h.	A.g., C.d., N.c., Flat, T.g., L.t., Ph.p.	All other species
larva	Noth., T.g.	L.t.	All other species
maple seed	T.g.	C.e.	All other species
oak leaf	L.c.	T.g., C.h., C.d.	All other species
pistachio	All other species	Pointy, P.c.	T.m., S.g.
plum	T.m.	P.c., P.f.	All other species
rose petals	O.c.	C.h.	All other species
sumach	All other species	T.s., Noth., L.c.	P.c., Pointy, S.g.

Table 8-6: Tentative dietary inferences based on analysis of gaps in raw Ω values: specific categories of food. See text for a description of the method used to determine adeptness. Species are listed in order of descending raw Ω values. See Appendix 1 for meaning of species abbreviations.

categories of food for this and all other analyses of correlation. On this plot, each kind of food constitutes a single series. I plotted the linear regression line for each series. The slope of the resulting trendline and the r-squared value were used to assess correlation. A large positive slope indicates there is a positive correlation between Seligsohn indices and fragmentation of the food in question. This correlation is strong if the r-squared value is large, and weak if it is small. R-squared values range from zero to one. If the slope of the trendline is negative, then there is a negative relationship between the Seligsohn indices and the fragmentation performances of the food in question. Figure 8-6 shows the correlation between the mean of six Seligsohn indices and fragmentation of four kinds of food. Only those foods that correlated strongly are shown (i.e., herbaceous foods and nuts/seeds were omitted). Seligsohn's main indices correlated relatively strongly and positively with the fragmentation of insects and meat. They correlated strongly and negatively with the fragmentation of fruit and gum.

Two of these correlations, that with the fragmentation of insects and that with the fragmentation of fruit, were predicted by Seligsohn (1977). The lack of strong correlation with performances on herbaceous foods was also predicted by Seligsohn.

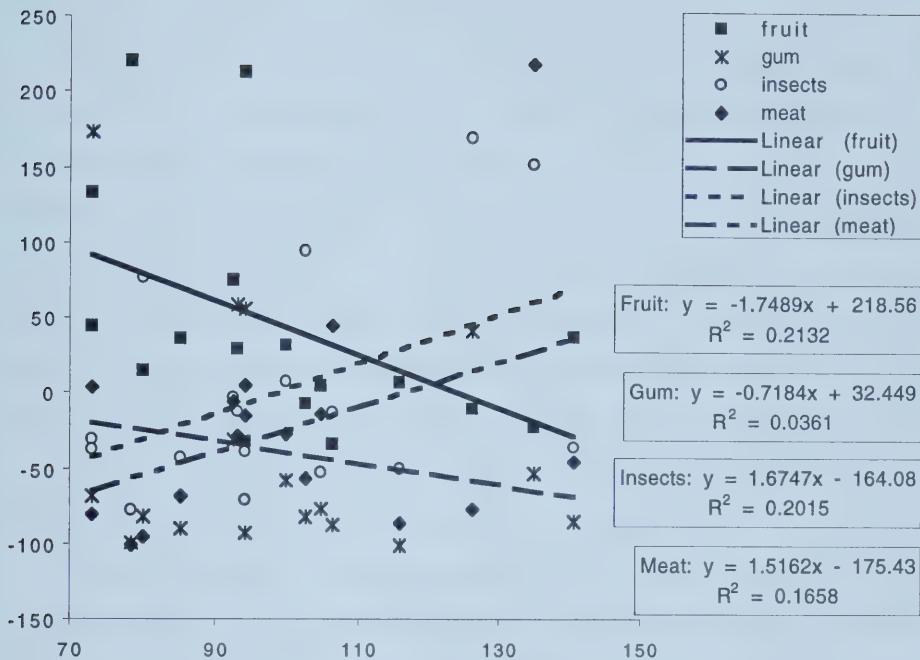


Figure 8-6 Correlation between Seligsohn's six main indices and fragmentation of food.
 Series consist of doubly averaged Ω values (x-axis). There is one series for each general category of food. Each datum point is the performance of one species for one kind of food. Trendlines result from linear least squares regressions performed in Microsoft Excel 98. The mean of six Seligsohn indices is on the y-axis. Strong correlations only are shown.

The remaining correlations were not predicted by Seligsohn, perhaps because he did not consider the consumption of gum or meat in his study. Attempts to fit polynomial, logarithmic and power functions to these series yielded no better correlations.

I treated Seligsohn's index XXXV separately because the predictions he made about it were different from those of the other six useful indices. I repeated the correlation test (above) for this index. Results are shown in Figure 8-7. There is a strong negative correlation between this index and the fragmentation of meat, and a weak positive correlation with the fragmentation of nuts and seeds. Those species that scored very highly for index XXXV fragmented nuts and seeds effectively, but fragmented meat

ineffectively. As Seligsohn predicted, index XXXV varied positively with the fragmentation of herbaceous foods and varied negatively with the fragmentation of insects; however, neither correlation was strong.

I scrutinized the results from my use of Kay's (1975) morphometric methods in a similar manner. I plotted factors 1, 2 and 3 from my principal components analysis (Chapter 4) against 'herbinsectivory'. This is a measure of the effectiveness of breaking down insects or herbaceous foods relative to the effectiveness of breaking down fruit. Kay claimed that his method separates those primates specializing on insects *or* leaves from those primates specializing on fruits. To measure 'herbinsectivory', I added 100 to each doubly averaged Ω value for herbaceous foods, insects and fruits. This renders all values positive. Then for each species, I added the value for herbaceous foods to that of insects and divided the sum by the value for fruits. This procedure gave 'herbinsectivory', plotted on the x-axis of Figure 8-8.

Of the three factors examined, only Factor 1 correlated strongly with herbinsectivory. The correlation was negative. Therefore those species that scored highly for Factor 1 performed well on fruit relative to insects and herbaceous foods.

For each species, I tested the correlation of herbinsectivory to each of the six initial measurements from Kay (1975). None of these measurements correlated strongly with herbinsectivory ($R^2 < 0.1$).

Because Kay's method focuses on herbaceous foods, insects and fruit, I tested whether or not Factors 1, 2 and 3 correlate with the fragmentation of these foods individually. Figures 8-9 and 8-10 show the results. Fragmentation of herbaceous foods is strongly negatively correlated to factor 3 from my Kay-style principal components analysis (Figure 8-9). Factor 3 is also strongly negatively correlated to the fragmentation of insects (Figure 8-10).

I also tested whether or not the factors from my principal component analysis correlate to the fragmentation of other kinds of food. Factor 3 correlated strongly and negatively with the fragmentation of nuts and seeds. Factor 1 correlated strongly and positively with the fragmentation of meat.

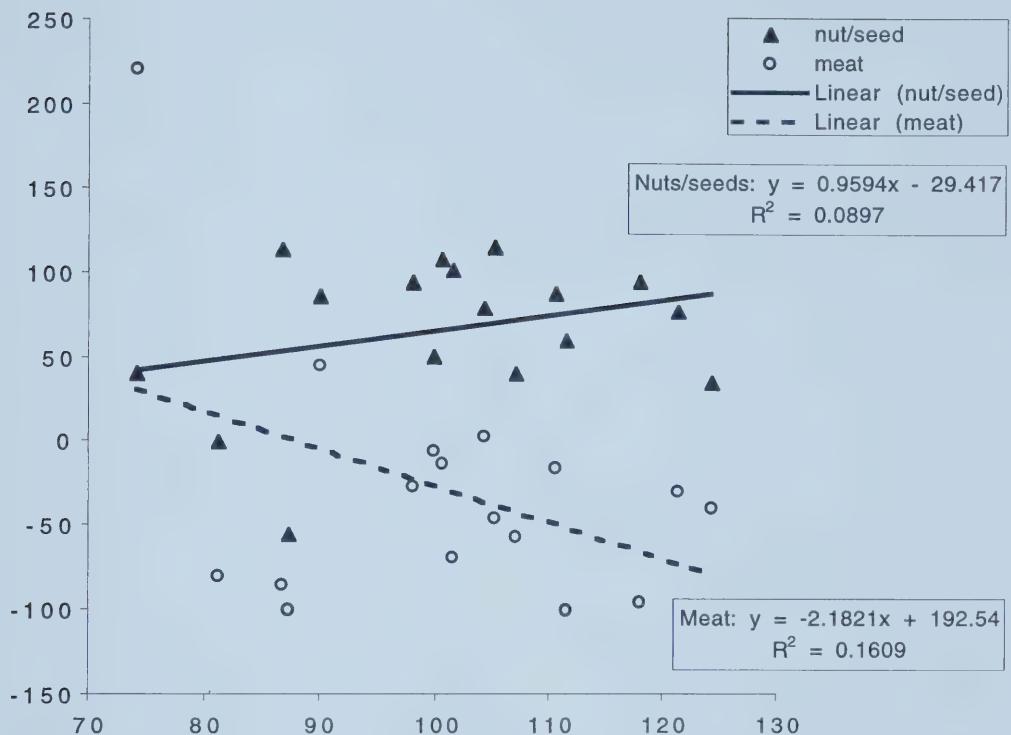


Figure 8-7 Correlation between Seligsohn index XXXV and fragmentation of food. As for Figure 8-6.

In Chapter 9 (section 9.7.2.), each principal component (=factor) is explained with reference to its morphological meaning. Inferred from tests of correlation, the relationship of each factor to diet is also discussed.

I tested the correlation between my application of Evans and Sanson's method and experimental fragmentation of general categories of food. I was particularly interested in the correlation with the fragmentation of insects because Evans and Sanson (1998) predicted that sharp cusps with sharp tips are best for breaking down hard-bodied insects and that sharp cusps with any kind of tip (though sharper cusp tips break more easily when they encounter resistant foods) are best for breaking down soft-bodied insects.

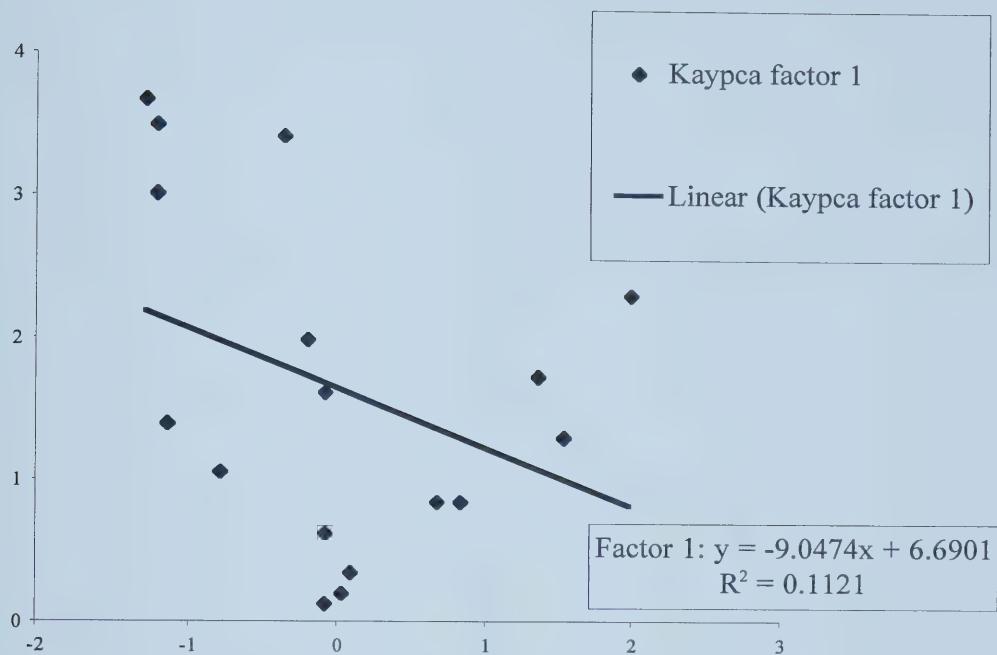


Figure 8-8 Correlation between principal component 1 and ‘herbinsectivory’.

‘Herbinsectivory’ (see text) is plotted on the y-axis. Factor 1 from my principal components analysis is on the x-axis.

Figures 8-11 through 8-14 show the results of this test of correlation. As predicted, fragmentation of insects correlates positively with cusp sharpness (i.e., negative correlation with cusp volume). It also correlates positively with tip sharpness (i.e., negative correlation with mean radius of curvature). Neither correlation is strong, however (Figure 8-11). Cusp sharpness and tip sharpness also correlate positively with fragmentation of meat; this correlation is stronger (Figures 8-11 and 8-12).

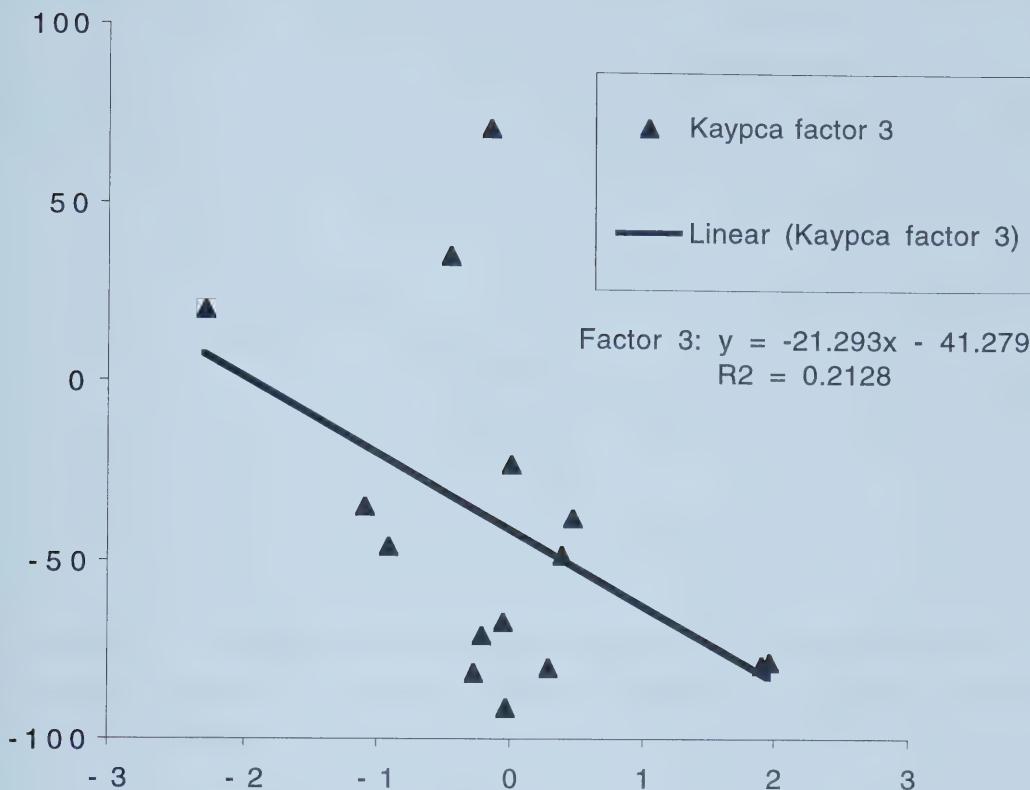


Figure 8-9 Correlation between principal component 3 and fragmentation of herbaceous foods. Factor 3 is plotted on the x-axis and doubly averaged Ω values are on the y-axis. Each datum point represents the value for one species. Trendlines are calculated as in Figure 8-6.

To tease out the relative influences of each kind of insect on these correlations, I tested the correlation of tip sharpness and cusp sharpness with the fragmentation of larvae and with the fragmentation of crickets (Figures 8-13 and 8-14). As predicted, sharp cusp tips (i.e., low values of mean radius of curvature) correlate positively with the fragmentation of the hard-bodied crickets and negatively with soft-bodied meal worms (Figure 8-13). Neither correlation is very strong. However, Figure 8-14 shows that although sharp cusps are good for fragmenting crickets, they are bad for fragmenting meal worms. This last result is *contrary* to the predictions of Evans and Sanson (1998).

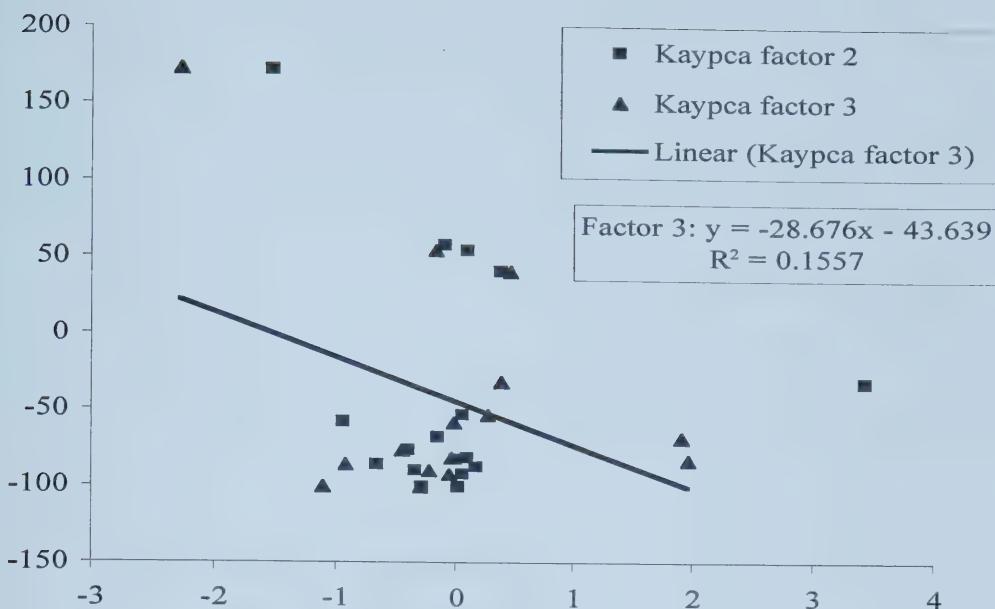


Figure 8-10 Correlation between principal components 2 and 3 and fragmentation of insects. As for Figure 8-9. Non-linear trendlines result from fitting a second order polynomial to the series in question.

8.3.2 Non-parametric methods

The correlations in section 8.3.1 are based on only a few datum points. Therefore, a few outliers may have a very large effect on r-squared values and equations for trendlines. To compensate for these influences, I used Kendall's rank correlation method on my data (see Bailey, 1997, pp. 184-188). I ranked test species with respect to masticatory performances of each kind of food and with respect to each morphometric method. Only relevant comparisons were made; that is, between a given morphometric method and breakdown of the foods about which it makes predictions. For example, the correlation between cusp sharpness and breakdown of insects was assessed, but not the correlation between cusp sharpness and breakdown of herbaceous foods.

Because Kendall's rank correlation test is designed for samples smaller than ten, it was necessary to use a normal approximation to test the significance of correlations (see Bailey, 1997, p. 185). The results of this test of correlation are listed in Table 8-7. A test statistic that has a p-value of 0.1 or more was judged to be insignificant. Using this

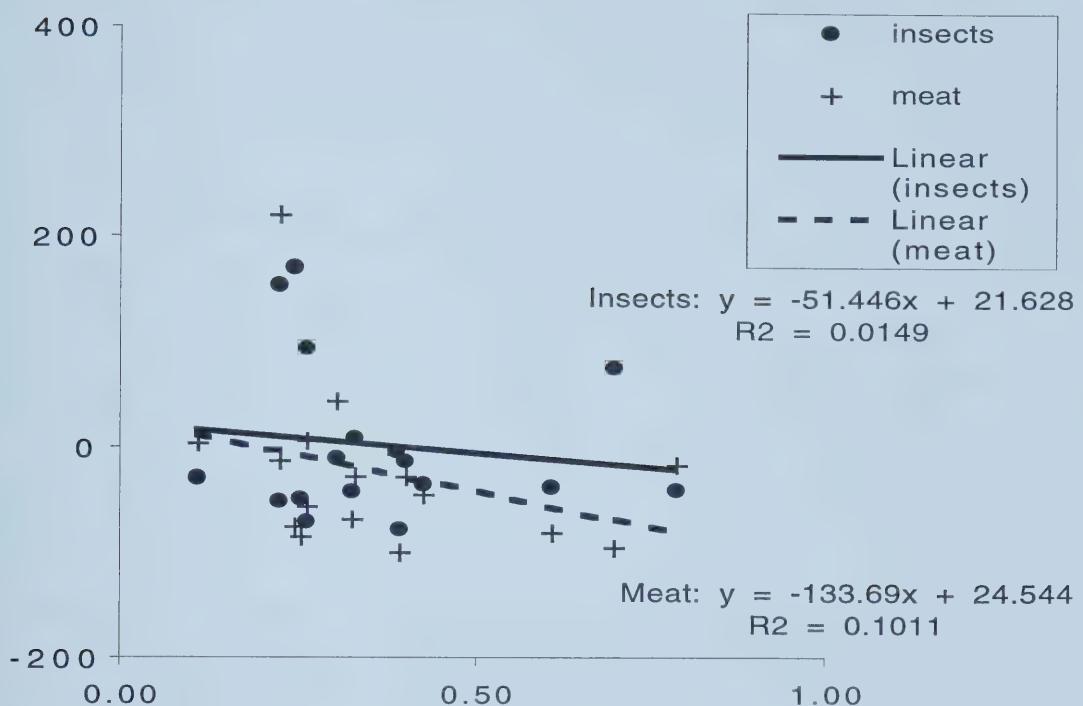


Figure 8-11 Correlation between mean radius of curvature (selected cusps) and fragmentation of insects and meat. Mean radius of curvature (mm) is on the x-axis and doubly averaged Ω values for insects and for meat are on the y-axis. Radius of curvature is equivalent to the ‘bluntness’ of the tip of a cusp.

criterion, all but one of the comparisons was insignificant: as predicted, the mean of Seligsohn’s six main indices correlated negatively with the breakdown of fruit ($p < 0.5$). This correlation is also expressed by Figure 8-6. All other correlations were insignificant.

A positive correlation between the mean of Seligsohn’s six main indices and the breakdown of insects was present, but insignificant. As predicted, Seligsohn’s index XXXV correlated positively with the breakdown of herbaceous foods; contrary to predictions, XXXV also correlated positively with the breakdown of insects.

Principal component 1 from Kay’s method correlated negatively with herbinsectivory. Thus, low, small second molars with lots of area for crushing and grinding are inferred to be better processors of insects and/or herbaceous foods, relative

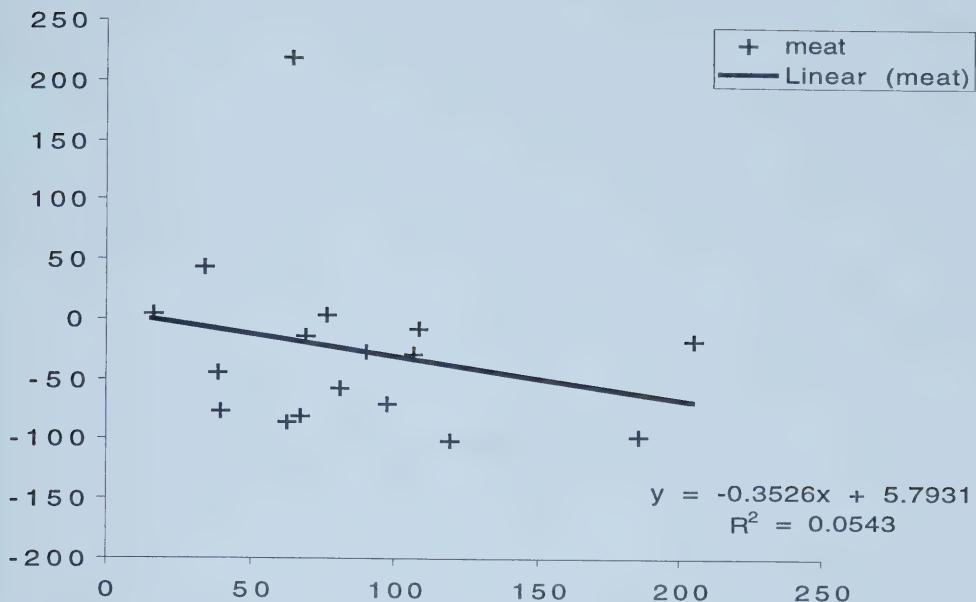


Figure 8-12 Correlation between cusp volume (selected cusps) and fragmentation of meat. Cusp volume at 10mm from the tip (mm^3) is on the x-axis and doubly averaged Ω values for meat are on the y-axis. Cusp volume is equivalent to the ‘bluntness’ of a cusp.

to fruit. Principal components (or Factors) 2 and 3 both correlated positively with herbinsectivory. Thus, high crowned second molars with lots of vertical shear and second molars with lots of shear generally break down fruits successfully (relative to insects and/or herbaceous foods). All three principal components correlated negatively with the breakdown of herbaceous foods; therefore, the breakdown of insects and fruits have the greatest impact on correlations between principal components and herbinsectivory. The breakdown of insects correlated negatively with principal component 1 and positively with principal component 2 and 3. The breakdown of fruit correlated positively with principal component 1 and negatively with principal components 2 and 3.

It is difficult to say whether or not these correlations match Kay’s predictions because the principal components in his analysis were quite different (i.e., their relationship with his six original measurements is quite different than the relationship between my three principle components and the same six original measurements).

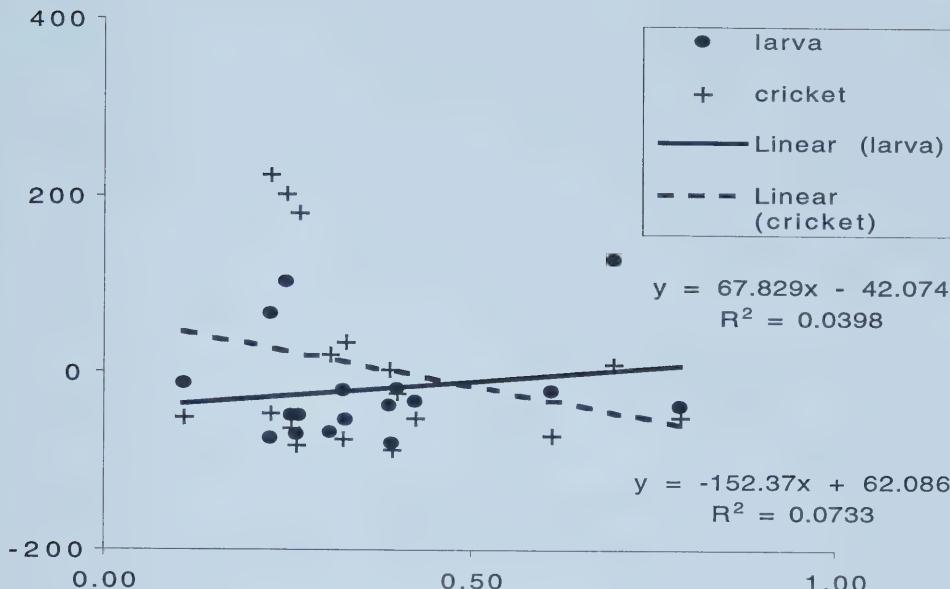


Figure 8-13 Correlation between radius of curvature (selected cusps) and fragmentation of larvae (i.e., meal worms) and crickets. As for Figure 8-11.

However, low, small molars with lots of area for crushing and grinding are generally thought to be effective in breaking down fruit but not insects or leaves. High crowned molars with lots of shearing planes are thought to be effective in breaking down insects or leaves but not fruit (e.g., Kay, 1975). The results of my test of correlation support these assumptions, albeit not significantly.

Evans and Sanson predicted that cusp sharpness would correlate positively with the breakdown of soft-bodied insects (e.g., larvae) and other ductile foods. Though not one of them is significant, the results of my test of correlation show that there is a positive relationship between cusp sharpness and breakdown of insects and especially larvae (i.e., meal worms). There is a negative correlation between cusp sharpness and breakdown of fruit. Evans and Sanson also predicted that there is a positive relationship between the sharpness of cusp tips and breakdown of insects, especially hard-bodied insects (e.g., crickets). Table 8-7 shows that this is, in fact, the case.

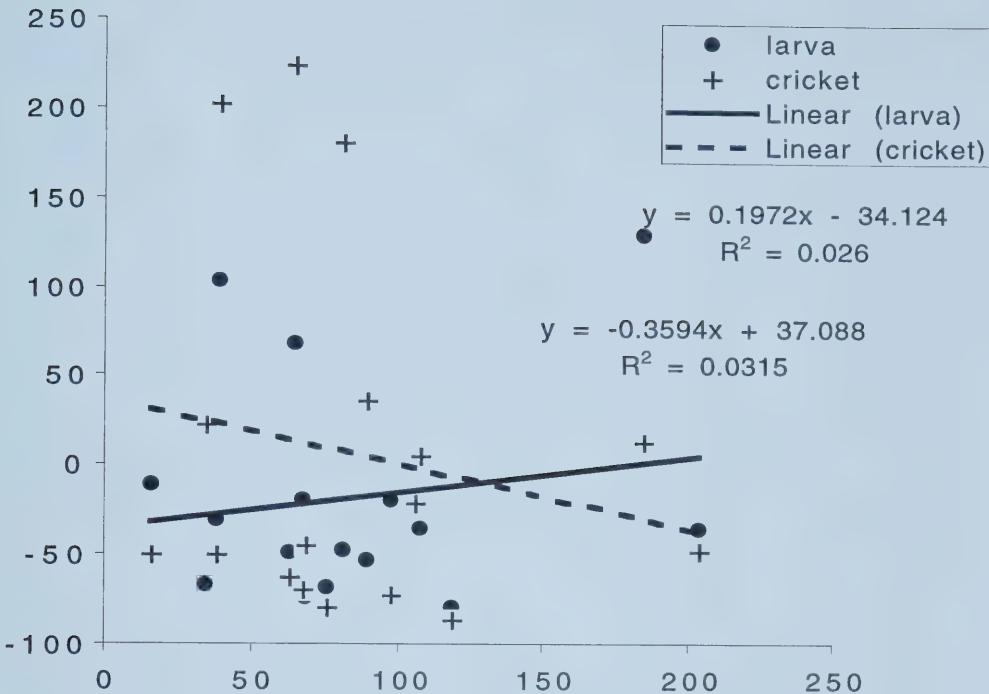


Figure 8-14 Correlation between cusp volume (selected cusps) and fragmentation of larvae (i.e., meal worms) and crickets. As for Figure 8-12.

8.4 Alternative methods for analyzing fragmentation

Though it seems most theoretically sound to express the effectiveness of fragmentation as the increase in surface area relative to volume, there are many other ways to express it. Sedimentologists use several methods to analyze the grain size distribution of unconsolidated sediments. I applied three of these methods to my samples of food fragments. I compared the results of these methods to the results of the above method to infer ‘diet’ in the taxa tested (see Chapter 9 for these dietary inferences).

The *graphic mean* of a sediment sample roughly approximates the mean particle size for that sample. An effective bout of chewing should produce a sample composed of small particles; therefore, the graphic mean for that sample should be small. *Sorting* is a

breakdown of...	morphometric measure	d (test stat)	p-value
fruit	Seligsohn's VI-VIII, XXVI-XXVIII	-2.183	0.05
insects	Seligsohn's VI-VIII, XXVI-XXVIII	0.371	insignificant
herbaceous	Seligsohn's XXXV	1.277	insignificant
insects	Seligsohn's XXXV	1.359	insignificant
herbinsectivory	Kay's method, PCA Factor 1	-1.524	insignificant
herbinsectivory	Kay's method, PCA Factor 2	1.195	insignificant
herbinsectivory	Kay's method, PCA Factor 3	1.112	insignificant
insects	Kay's method, PCA Factor 1	-0.783	insignificant
insects	Kay's method, PCA Factor 2	1.112	insignificant
insects	Kay's method, PCA Factor 3	0.865	insignificant
fruit	Kay's method, PCA Factor 1	1.112	insignificant
fruit	Kay's method, PCA Factor 2	-0.453	insignificant
fruit	Kay's method, PCA Factor 3	-1.195	insignificant
herbaceous	Kay's method, PCA Factor 1	-0.536	insignificant
herbaceous	Kay's method, PCA Factor 2	-0.700	insignificant
herbaceous	Kay's method, PCA Factor 3	-1.277	insignificant
fruit	cusp sharpness	-0.536	insignificant
insects	cusp sharpness	0.371	insignificant
larvae	cusp sharpness	0.453	insignificant
insects	tip sharpness	0.371	insignificant
crickets	tip sharpness	1.195	insignificant
larvae	tip sharpness	-0.536	insignificant

Table 8-7 Results of a test of correlation between morphometric data and masticatory performances. Correlation is tested using Kendall's rank correlation method (Bailey, 1997). A negative d-value indicates that the correlation is negative. A p-value of 0.10 or more is judged insignificant.

measure of the spread among grain sizes (Levinton, 1995). It can be measured several ways, but it is usually considered the total amount of deviation from the graphic mean. An effective – but short - bout of chewing, as in my experiment, should result in a good spread of particle sizes. Therefore effective fragmentation is equivalent to good sorting in this experiment. This is corroborated by the fact that the performances with the highest Ω values and the lowest graphic means generally have the poorest sorting. As the number of chewing cycles increases to a biologically realistic number (i.e., much more than ten cycles), sorting should actually *decrease* as all fragments are reduced to a uniformly small size (but see Alexander, 1998). Although it is probably not relevant in

this experiment, a low sorting value (with a small graphic mean) may also indicate highly effective chewing.

To calculate the graphic mean and sorting of a sample, grain sizes must be converted to phi (Φ) sizes. The following equation (from Folk and Ward, 1957) is used:

$$\Phi = -(\log_2 G) \quad (8-8)$$

where G is grain size in millimetres. Smaller phi values refer to larger grains.

The diameter of each fragment in a given sieve is assumed to be equal to the sieve's aperture size. For each sample, the total mass of fragments in a given sieve is expressed as a percentage of the total mass of the sample. Percentage values for each sieve are then converted to 'percent finer than' values. The 'percent finer than' value for the finest sieve is equal to that sieve's percentage value; the 'percent finer than' value for the next finest sieve is equal to the sum of that sieve's percentage value and the percentage value for the finest sieve; etc. 'Percent finer than' values are plotted against phi values and an s-curve is fitted to the data. The equation of this curve can be used to calculate the graphic mean and the sorting (as well as other values, such as skewness and kurtosis) of the sample. I used a line instead of an s-curve. The s-curve is linear except at very high and very low 'percent finer than' values, therefore a line is a reasonable approximation.

The graphic mean is approximated using:

$$M = (\Phi_{16} + \Phi_{50} + \Phi_{84}) / 3 \quad (8-9)$$

where M is the graphic mean, Φ_{16} , Φ_{50} and Φ_{84} are the phi values at 16% finer than, 50% and 84% respectively (Folk and Ward, 1957). The graphic mean for each species and each general category of food are shown in Figure 8-21.

The sorting of a sample is calculated using the following equation:

$$\text{Sorting} = -[(\Phi_{84} - \Phi_{16}) / 4] - [(\Phi_{95} - \Phi_5) / 6.6] \quad (8-10)$$

Values of sorting for each species and general category of food are depicted graphically in Figure 8-22.

For the purpose of comparison, I have included a graphic representation of the doubly averaged Ω values for all species and general categories of food (Figure 8-23).

Another common method of representing the grain size character of a sedimentary matrix is the use of ternary diagrams. These are essentially triangular plots of three

variables. The variables most commonly used in sedimentology are the percentages of sand, silt and clay in a given sample. Instead, I used granules, sand and silt because of the large size of most fragments in my samples. I generated a ternary diagram for each general category of food. Each species is represented by a single datum point on each diagram. The percentage of granules is the mass of granule-sized particles (2.83mm or more in diameter) in a single test sample divided by the total mass for that sample. Particles 0.991mm or larger are considered sand and particles less than 0.991mm in diameter are considered silt. Although these diameters do not correspond exactly to those normally used in sedimentology, they are convenient here because they correspond to aperture sizes of sieves used in the mastication experiment.

For all general categories of food, most points clustered at the ‘percentage granule’ apex because most of the masticated food remained as large particles. This made it difficult to assess the effectiveness of fragmentation in different species. To solve this problem, I adjusted the scale on each axis until most datum points were discernable, and then plotted the ternary diagrams again. However, not all points could be shown and labeled on ternary diagrams; therefore, the source data are presented after the diagrams (Table 8-8). Ternary diagrams presented here (Figures 8-15 to 8-20) show the relative percentages of ‘granules’, ‘sand’ and ‘silt’ for most test species. Each general category of food is shown in a separate diagram.

Dietary inferences are made in Chapter 9 based on a comparison of the data from all statistical methods described above. Particular weight is given to Ω values and ternary diagrams. These two methods are particularly sound because the assumptions they rely on are the same or similar to the way in which masticatory performance is defined (Bates *et al.*, 1976).

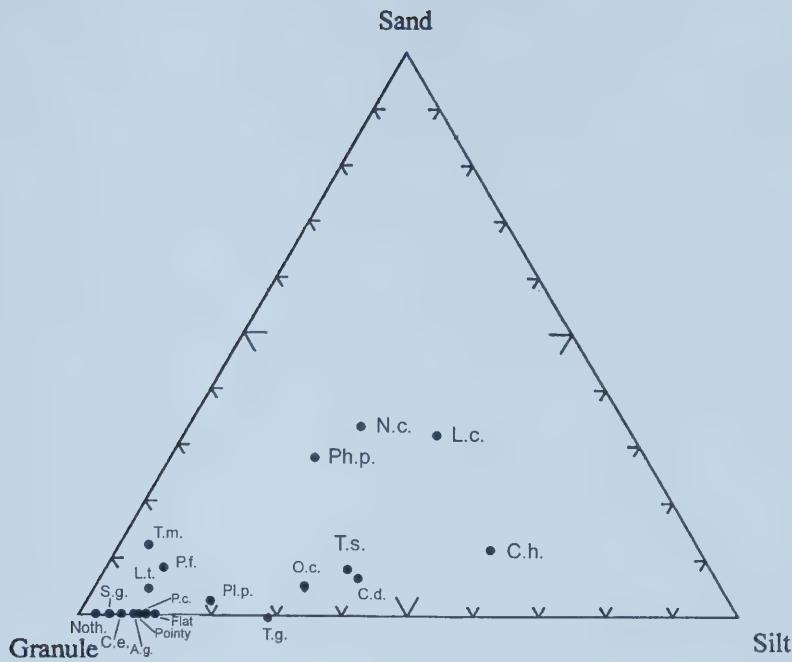


Figure 8-15 Ternary diagram for herbaceous foods. See text for explanation. See Appendix 1 for abbreviations of species names. Not all datum points are discernable; therefore, see Table 8-8 for source data. Scale for granules: 90-100%; sand: 0-10%; silt: 0-10%.

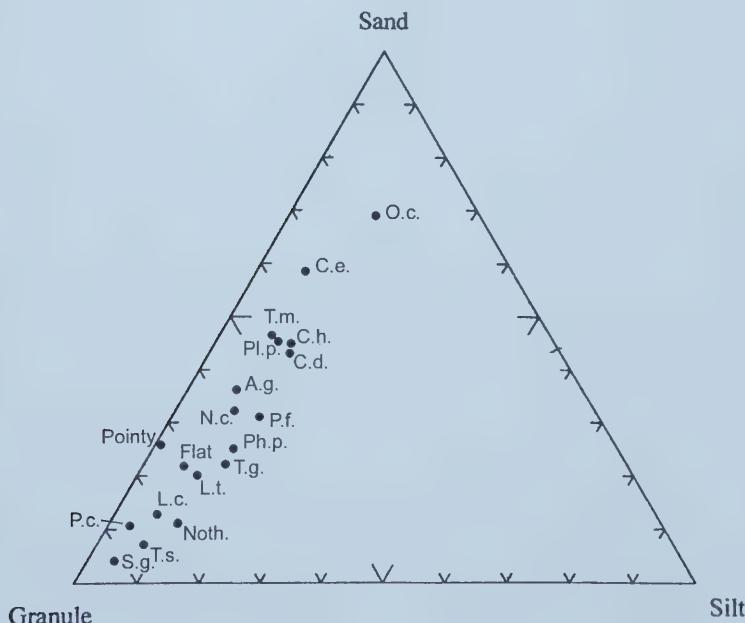


Figure 8-16 Ternary diagram for nuts and seeds. As for Figure 8-15. Scale for granules: 50-100%; sand: 0-50%; silt: 0-50%.

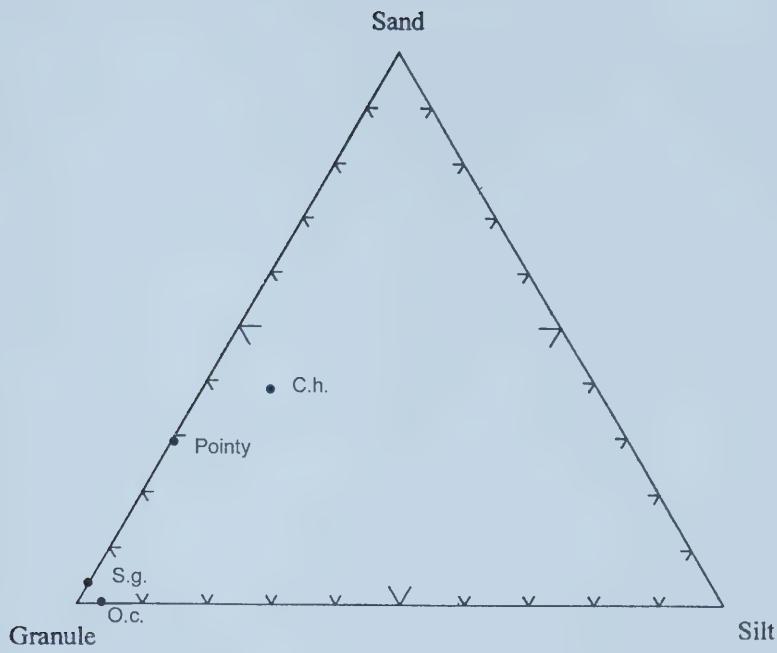


Figure 8-17 Ternary diagram for gum. As for Figure 8-15. Scale for granules: 95-100%; sand: 0-5%; silt: 0-5%.

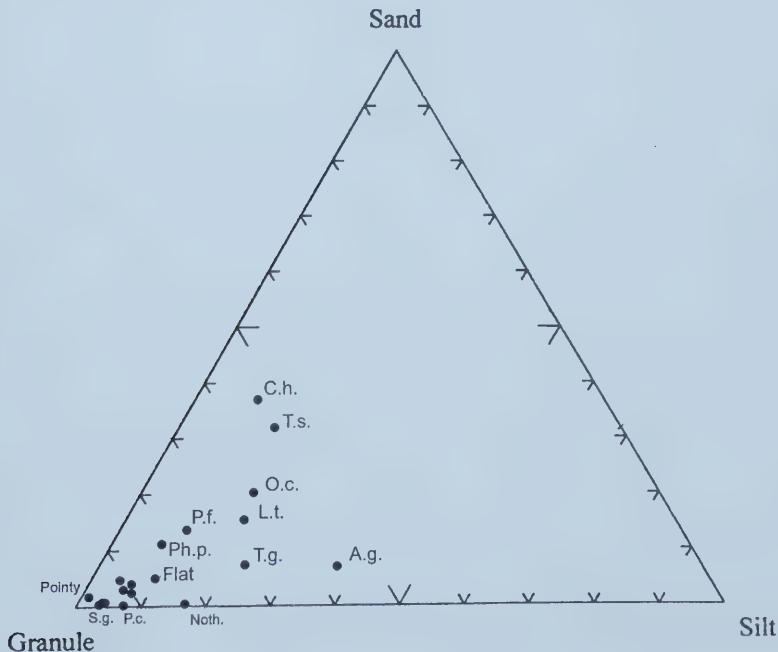


Figure 8-18 Ternary diagram for insects. As for Figure 8-15. Scale as for Figure 8-15.

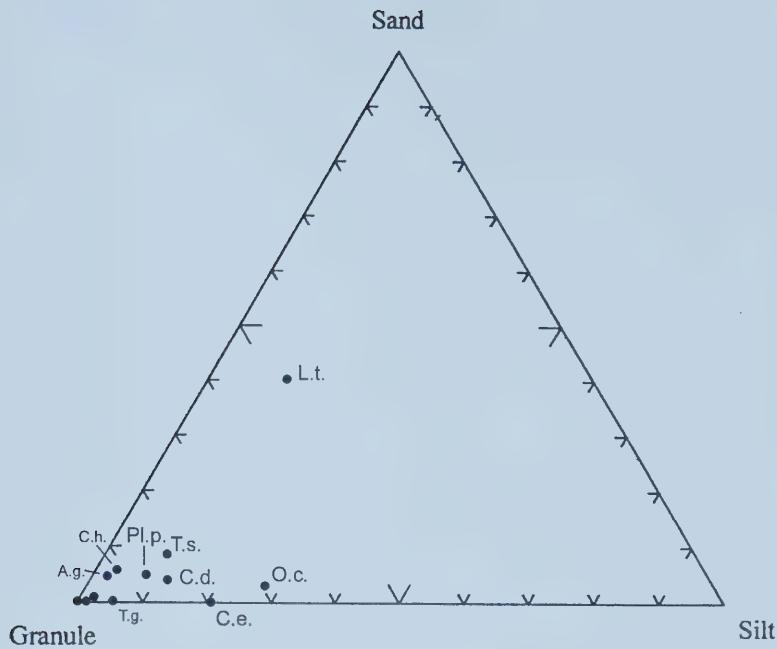


Figure 8-19 Ternary diagram for meat. As for Figure 8-15. Scale as for Figure 8-15.

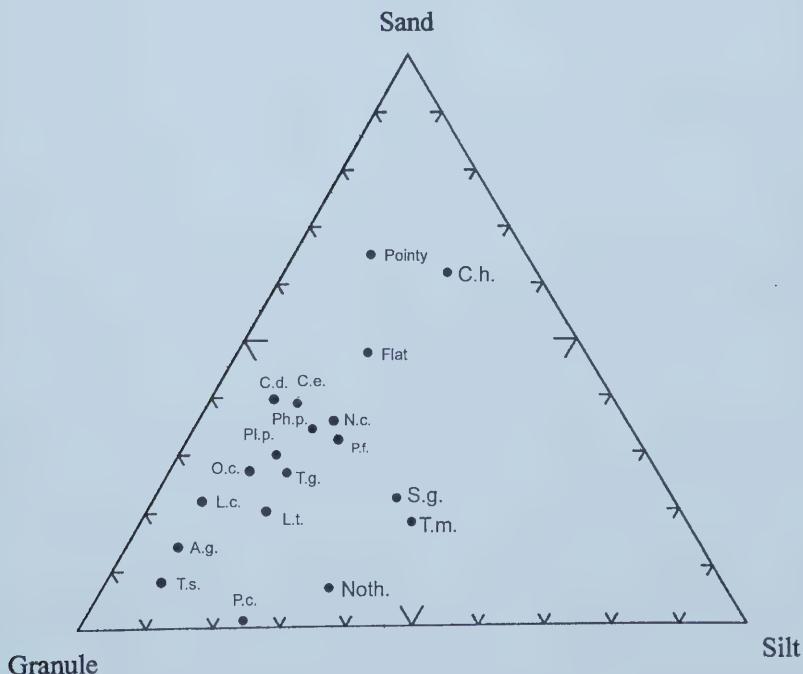


Figure 8-20 Ternary diagram for fruit. As for Figure 8-15. Scale as for Figure 8-15.

	HERBACEOUS		NUTS/SEEDS			GUM			
species	% granule	%sand	%silt	% granule	%sand	%silt	% granule	%sand	%silt
<i>A. g.</i>	99.4	0.0	0.6	78.1	18.6	3.3	100.0	0.0	0.0
<i>C. e.</i>	99.4	0.0	0.6	66.8	29.3	3.9	100.0	0.0	0.0
<i>C. h.</i>	93.1	1.2	5.7	71.8	21.9	6.4	97.5	2.0	0.5
<i>C. d.</i>	95.4	0.6	4.0	74.4	21.4	4.3	99.9	0.0	0.1
<i>Flat</i>	98.9	0.0	1.1	86.0	10.4	3.7	100.0	0.0	0.0
<i>L. c.</i>	93.0	3.2	3.7	90.0	7.3	2.7	99.8	0.0	0.2
<i>L. t.</i>	98.7	0.4	0.9	85.1	10.8	4.1	99.9	0.0	0.1
<i>Noth.</i>	99.8	0.0	0.2	89.5	6.7	3.8	100.0	0.0	0.0
<i>N. c.</i>	94.1	3.3	2.7	79.2	16.4	4.4	99.9	0.0	0.1
<i>O. c.</i>	96.3	0.2	3.5	58.7	35.5	5.8	99.7	0.0	0.3
<i>Ph. p.</i>	95.1	2.8	2.1	83.4	12.5	4.1	100.0	0.0	0.0
<i>P. c.</i>	99.0	0.0	1.0	92.9	6.1	1.0	99.9	0.0	0.1
<i>P. f.</i>	98.6	0.1	1.3	78.6	15.6	5.8	99.8	0.0	0.2
<i>Pl. p.</i>	97.9	0.0	2.0	73.3	22.9	3.8	100.0	0.0	0.0
<i>Pointy</i>	99.3	0.0	0.7	87.0	12.4	0.6	98.5	1.5	0.0
<i>S. g.</i>	99.6	0.0	0.4	96.6	3.1	0.3	99.8	0.2	0.0
<i>T. s.</i>	95.6	0.8	3.6	92.3	4.4	3.3	100.0	0.0	0.0
<i>T. m.</i>	98.5	0.1	1.4	74.5	23.0	2.5	100.0	0.0	0.0
<i>T. g.</i>	97.0	0.0	3.0	84.6	10.3	5.2	99.7	0.0	0.3
	INSECTS			MEAT			FRUIT		
species	% granule	%sand	%silt	% granule	%sand	%silt	% granule	%sand	%silt
<i>A. g.</i>	95.7	0.7	3.6	99.4	0.3	0.3	98.0	1.2	0.8
<i>C. e.</i>	99.2	0.0	0.8	98.0	0.0	2.0	94.8	3.9	1.3
<i>C. h.</i>	95.4	3.7	0.9	99.2	0.5	0.3	91.5	6.2	2.3
<i>C. d.</i>	99.1	0.3	0.6	98.4	0.2	1.3	94.9	4.0	1.0
<i>Flat</i>	98.4	0.5	1.0	99.8	0.0	0.2	93.2	4.8	2.0
<i>L. c.</i>	99.5	0.1	0.4	99.8	0.0	0.2	97.0	2.2	0.7
<i>L. t.</i>	96.8	1.4	1.8	94.9	4.0	1.1	95.4	3.0	1.6
<i>Noth.</i>	98.4	0.0	1.6	100.0	0.0	0.0	96.2	2.0	1.8
<i>N. c.</i>	99.0	0.2	0.8	99.8	0.0	0.2	94.4	3.6	2.0
<i>O. c.</i>	96.3	2.0	1.7	97.0	0.2	2.8	96.0	2.6	1.3
<i>Ph. p.</i>	98.2	1.1	0.7	99.8	0.0	0.2	94.8	3.4	1.7
<i>P. c.</i>	99.2	0.0	0.8	99.8	0.2	0.1	97.4	0.2	2.4
<i>P. f.</i>	97.6	1.3	1.1	99.6	0.0	0.4	94.4	3.3	2.3
<i>Pl. p.</i>	99.1	0.5	0.5	98.9	0.4	0.7	95.9	3.4	0.8
<i>Pointy</i>	99.8	0.1	0.1	99.6	0.0	0.4	92.4	6.4	1.2
<i>S. g.</i>	99.7	0.1	0.2	100.0	0.0	0.0	94.0	2.1	3.8
<i>T. s.</i>	95.3	3.1	1.6	98.3	0.7	1.0	98.5	0.8	0.7
<i>T. m.</i>	99.4	0.1	0.5	99.7	0.0	0.3	94.0	2.0	4.0
<i>T. g.</i>	97.1	0.7	2.3	99.5	0.4	0.1	95.4	2.8	1.8

Table 8-8 Source data for ternary diagrams. Appendix 1 lists the meanings of abbreviations for species names.

8.5 Qualitative results

All scientific inquiries are based on observations. Many of these observations are purely qualitative. Therefore the scientific role of qualitative data should not be minimized. Quantitative data are easily communicated and they are deduced by supposedly objective means. However, they are usually derived from what is *really* observed; that is, they arise as the result of interpretation or rationalization of initial *qualitative* observations.

The amount or proportion of food that is well fragmented was assessed above using quantitative methods. However, one of the virtues of an experiment like this one is that qualitative observations are also possible. In the course of this experiment, I observed *how* various kinds of food were broken down. I was able to observe how various features on the premolars and molars affect different parts of foods and how they affect foods of different material properties. This is particularly important to understanding the functional dental anatomy of the species tested. The disadvantage of qualitative observations is that they are more susceptible to human error and observer bias (though quantitative observations also are subject to these influences).

8.5.1 *Herbaceous foods*

In most cases, the ‘herbaceous’ parts of plants (i.e., leaves and petals) were poorly fragmented. Often these foods were distorted or torn without separation into smaller fragments. However, some dentitions were capable of breaking herbaceous foods into smaller parts. The most commonly occurring fragments were very small (<1mm diameter) polygons (usually roughly circular). These fragments were ‘punched-out’ of the leaf or petal as if by the action of a hole-puncher. Because I often found these fragments resting on the tips of cusps, I assumed that they were punched out by the cusp tips themselves. This phenomenon is particularly characteristic of the brittle oak leaves. It occurred most notably in *Carpodaptes hazelae*, *Loris tardigradus* and ‘Pointy’. *C. hazelae* and *L. tardigradus* have the sharpest cusp tips of all species measured.

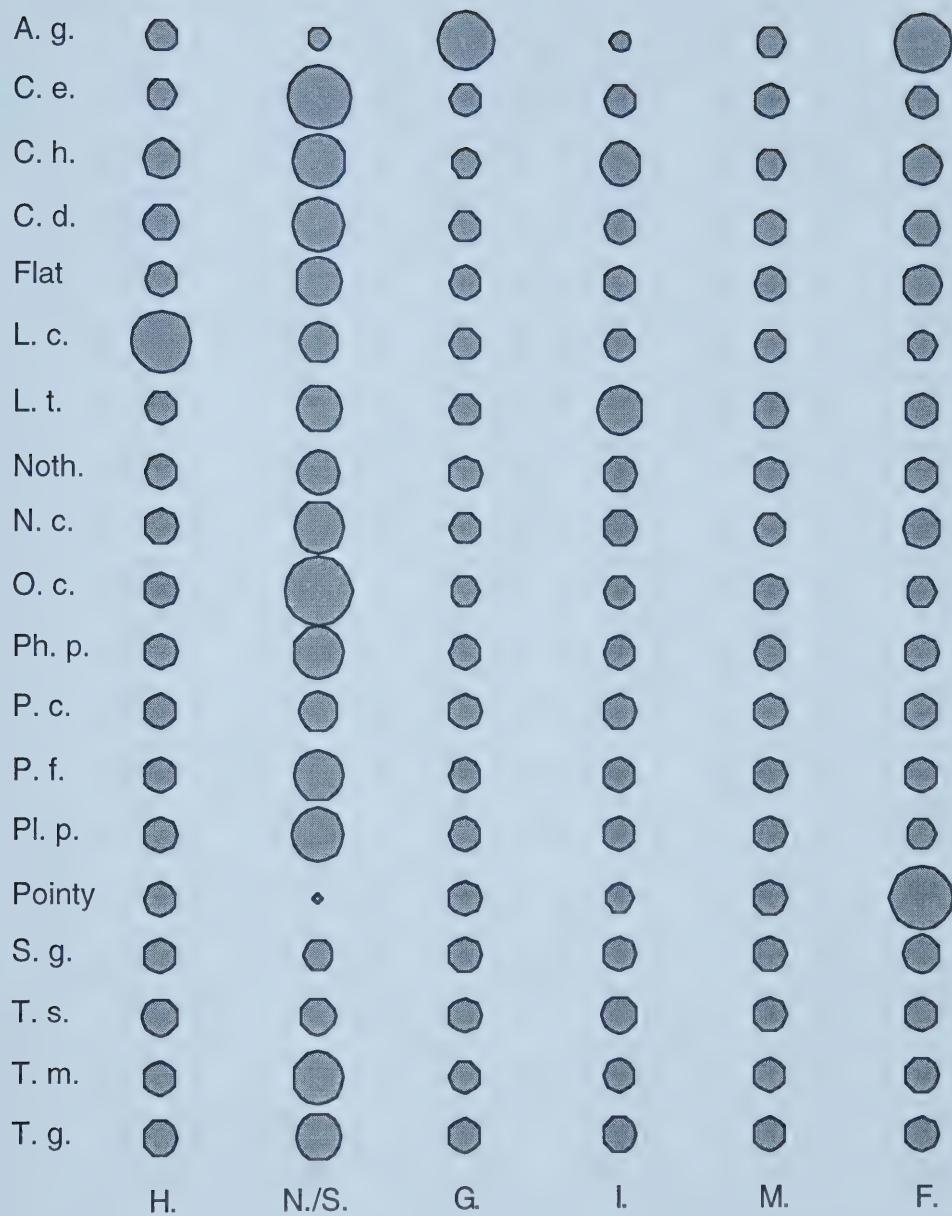


Figure 8-21 Graphic mean for each species and general category of food. The size of each bubble represents the effectiveness of fragmentation (i.e., $1 / \text{mean particle size}$). Food categories along the x-axis are as follows: herbaceous foods, nuts and seeds, gum, insects, meat, fruit. See Appendix 1 for abbreviations of species names. Graphic means are doubly averaged in the manner described above for Ω values.

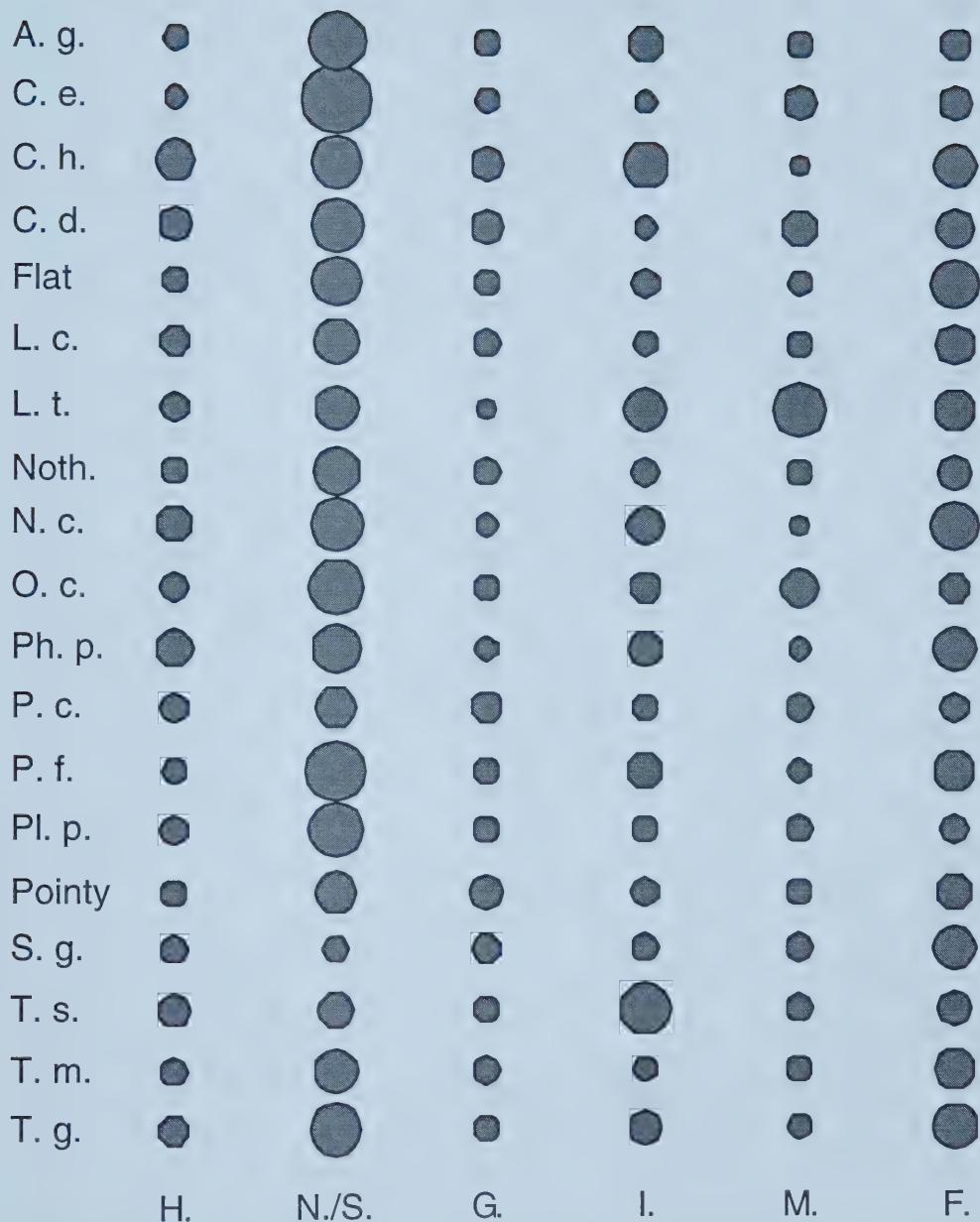


Figure 8-22 Sorting for each species and general category of food. The size of the bubble represents the effectiveness of fragmentation (i.e., $1 / \text{degree of sorting}$). Food abbreviations as for Figure 8-21. See Appendix 1 for abbreviations of species names. Sorting values are doubly averaged in the manner described above for Ω values.

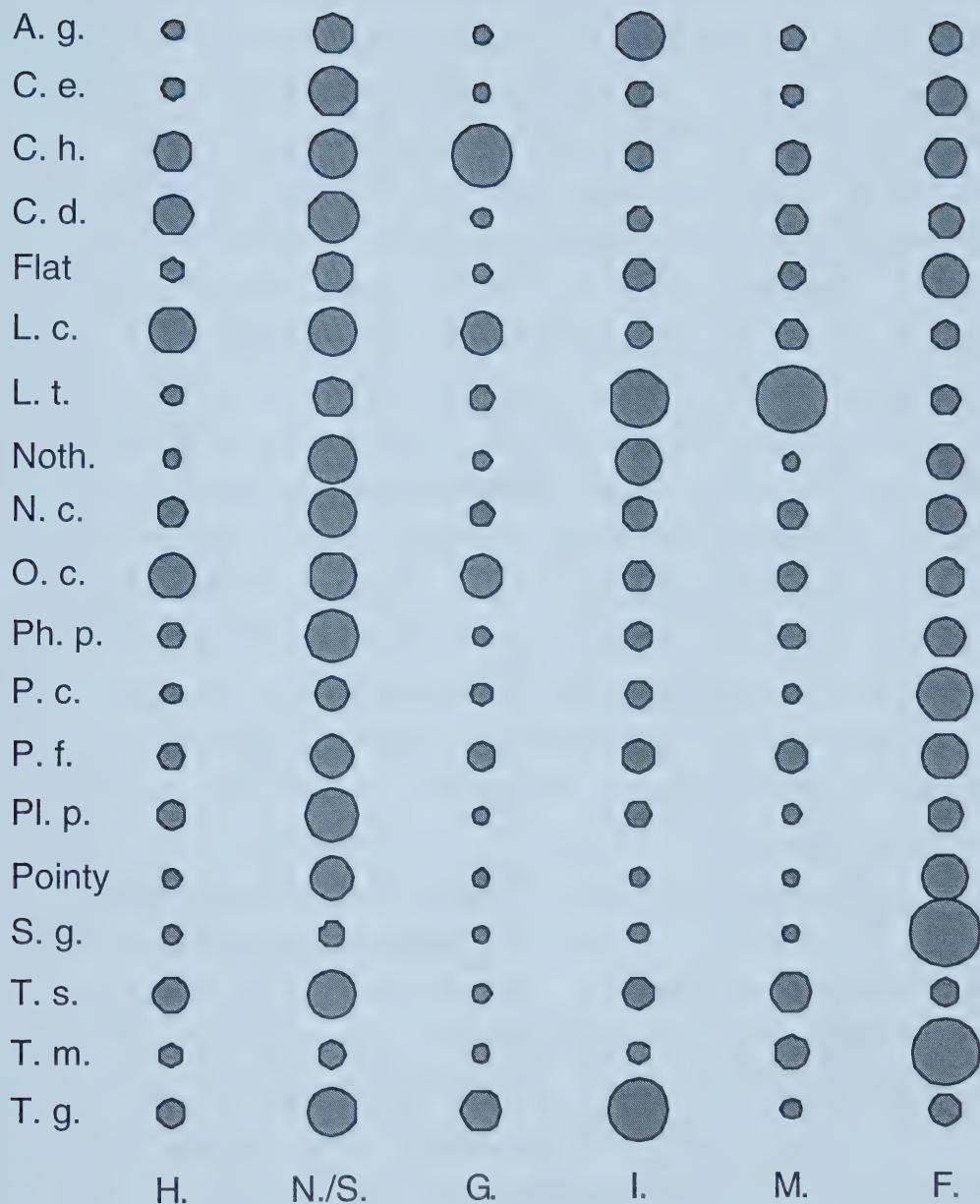


Figure 8-23 Doubly averaged Ω values for each species and general category of food.

The size of a bubble represents the effectiveness of fragmentation (i.e., the increase due to simulated mastication in the surface area to volume ratio of food). Food abbreviations as for Figure 8-21. See Appendix 1 for abbreviations of species names.

Small polygonal fragments also arose as ‘shrapnel’ when larger pieces were torn apart. The latter is the only explanation for the very small fragments that resulted from the mastication of oak leaves by the ‘Flat’ dentition.

In some cases, leaves and petals were shredded into small but substantial parts. Rose petals tore easily in any direction - except across their thickness. They are ‘fragile’, such that when a crack is initiated within a petal, it propagates rapidly (see Strait, 1997, for definitions of material properties of food). Rose petals were, therefore, the herbaceous food most susceptible to extensive fragmentation. The following species repeatedly shredded rose petals into substantial fragments: *Otolemur crassicaudatus*, *Carpolestes dubius*, and *Nycticebus coucang*. Both carpolestid dentitions seem regionally specialized as to function. The blade-like lower premolar was particularly effective at tearing leaves and petals, whereas the cuspidate molars separated the torn material into discrete fragments. Most other species seemed unable to fragment rose petals. Those that did were restricted to the ‘punch-out’ scenario described above.

Ginkgo leaves also were shredded into large strips by several species. However, these leaves were cut only in a single plane: parallel to the veins, never perpendicular. Specimens of *Lemur catta* and *Carpolestes dubius* excelled at shredding ginkgo leaves. Most other specimens punched out small fragments only or simply bent and mangled the leaves without fragmenting them. Ginkgo leaves are relatively pliant: they are easily distorted while resisting fragmentation.

Oak leaves were very poorly fragmented by all species except *Lemur catta* and perhaps *Carpolestes dubius*. The post-canine dentitions of these two species seemed capable of shredding oak leaves into fragments. All other species merely distorted or tore oak leaves. Some only punched out small fragments.

Oak leaves resisted fragmentation, probably because the veins – which run in different directions - impede the propagation of cracks through the leaf material. These leaves are relatively pliant when fresh; therefore, they do not suffer brittle failure. However, when they dry out, they become very brittle. Therefore, I have used only fresh leaves.

8.5.2 Nuts and seeds

The ‘nuts and seeds’ category is more heterogeneous than the ‘herbaceous foods’ category. It includes maple seeds, pistachios and sumachs. These individual foods have somewhat different material properties.

Maple seeds are somewhat brittle, tough and strong. They do not suffer crack propagation easily, nor are small pieces broken off with ease. However, they tend to shatter when a great deal of force is applied. Maple seeds generally break into long fragments along their long axis. However, they are heterogeneous: the endosperm is much more resistant than the seed coat.

Maple seeds were extremely poorly fragmented by the species tested here. Most dentitions merely dented them, though some small pieces were inevitably broken off the surface. The species capable of breaking open maple seeds were *Tupaia glis*, *Cantius eppsi* and *Carpodaptes hazelae*. The specimens assigned to these species often tore open the seed coat, and sometimes split the seed itself. *Carpodaptes hazelae*, in particular, often broke the entire food item in half perpendicular to its long axis. This occurred only when the maple seed sat upon the molar teeth, with its long axis in the transverse plane (perpendicular to the long axis of the tooth row). Neither carpolestid dentition was capable of holding a maple seed, a sumach or a pistachio chunk between the plagiualacoid p4 and the upper premolars. Perhaps the tongue performed this action in life.

Pistachios are particularly susceptible to crack propagation: they are fragile. They are also brittle, collapsing into fragments under small loads. I removed the pistachio shells prior to testing and tested only chunks of endosperm; therefore, the pistachio material tested was homogenous. It was necessary to remove the shell in order to cut the pistachio into smaller chunks (scaled down to the size of other kinds of food).

Based on qualitative assessment alone, it is very difficult to discriminate between good and bad fragmentation of pistachios. All performances appeared to be very good. Pistachio chunks were usually fragmented explosively within the first few chewing cycles. The largest fragments were replaced between the upper and lower teeth, and further fragmentation occurred. The resulting pistachio fragments were mostly nearly

spherical and represented a wide variety of sizes. Qualitatively, the least effective performances were that of *Smilodectes gracilis* and that of *Tetonius matthewi*.

Sumach fruits are more like nuts with respect to their material properties. The seed coat is covered with small hairs. It is pliant and resistant to fracture. Sumach fruits are disc-shaped. The seeds themselves (two or three) are ovoid; they are extremely hard, although they were broken in some instances.

Sumachs were fragmented moderately well. Most species at least managed to fragment the hairy seed coat, and many split the seed coat open, ejecting the seeds. The poorest performances resulted in small dents in the surface of the seed coat. The best performances were given by *Plesiolestes problematicus*, *Otolemur crassicaudatus* and to a lesser degree *Cantius eppsi*. *P. problematicus* is the only species that fragmented the seeds themselves. In most cases, a sumach supported along its circumference went unfragmented. Fragmentation occurred mostly when a sumach rested on its flat side.

8.5.3 Gum

I tested gum arabic only when it had reached a ‘toffee-like’ consistency; at this point it resembles the consistency favoured by bushbabies and many other gummivorous primates (Nash, 1989). At this consistency, gum is neither completely brittle nor completely ductile. When a small load is applied, it behaves in a ductile manner, but with increased load, brittle fracture may occur. As the surface of the gum is always drier than the inside, small fragments are easy to dislodge from the surface. Gum is easily penetrated by sharp cusps, but these only dent the gum – they fail to fragment it. For fragmentation to occur, it is necessary to drive a wedge clear through the thickness of the piece of gum. The fragments of gum that resulted from most tests were small pieces dislodged from the dry, brittle surface. However, some dentitions were capable of splitting the gum into significant fragments. All measures of the effectiveness of fragmentation used here relate to the mass of fragments multiplied by the inverse of the radius of the fragments. Therefore, having a few large fragments is much better than having a few small fragments.

Carpodaptes hazelae, *Carpolestes dubius* and to a lesser degree *Otolemur crassicaudatus* excelled at splitting gum. Gum was very well divided in carpolestids when the gum was placed over the plagiulaucoid blade. Other species merely dented, punctured or distorted gum samples. Varying consistencies, from soft and rubbery to dry and brittle, were fragmented approximately equally. In the latter condition, there were more minute fragments that were broken off the surface, but these were few and generally smaller than the minimum measurable size (diameter < 0.5mm).

8.5.4 Insects

The foods mentioned above are basically dry. Insects and fruits have a high liquid content. This complicates quantification of masticated fragments of insects and fruit. However, this complication is an unavoidable feature of primate food. When the liquid content of a masticated sample was high, I dried the sample under a lamp until all visible water had evaporated.

Insect bodies are structurally complex and heterogeneous. I attempted to standardize the size and preservational state of test insects. Both crickets and meal worms are covered with a resistant cuticle that surrounds a pulpy inside. The cuticle is structurally similar to that of a leaf. It resists crack propagation and brittle fracture; it is tough and ductile (though that of crickets is more brittle). The insides of both crickets and meal worms behaved much like a very viscous liquid or pulp. Most dentitions penetrated the cuticle successfully and expressed visceral juices. Also, most dentitions broke limbs off the bodies of crickets. However, only a few dentitions successfully fragmented meal worms, and only a few were capable of cutting cricket bodies into small fragments.

Meal worms are particularly ductile. Most dentitions merely distorted and flattened them. However, *Tupaia glis*, *Notharctus sp.*, *Carpodaptes hazelae* and *Tarsius spectrum* were all very successful at breaking meal worms into small fragments and expressing their juices.

The cuticle of crickets is somewhat brittle, though their insides are generally ductile (or completely yielding). Only one species, *Loris tardigradus*, fractured crickets

in the explosive and brittle fashion depicted by Strait (1997). Several other species broke both the cuticle and the viscera of crickets into substantial fragments. Particularly good examples are *T. spectrum* and *Otolemur crassicaudatus*.

8.5.5 Meat

Chicken breast muscle is particularly ductile, very resistant to crack propagation and relatively homogenous. This muscle was chosen, in part, because of its homogeneity. In most instances, chicken breast was very poorly fragmented. In an action akin to tenderizing, it was easily distorted and punctured by most dentitions. Some dentitions tore very small fragments off the exterior. These fragments were retrieved – with some effort - from deep within talonid basins. Perhaps hyper-carnivorous mammals have few molar cusps because raw meat tends to get stuck between cusps and is lost to digestion.

Loris tardigradus fragmented meat more effectively than did any other species. This species' dentition regularly divided the chicken into smaller chunks and additional tiny fragments. It was closely followed by both carpolestids. During every test, the plagiualacoid p4 punched through the entire muscle mass. Given more chewing cycles and precise placement of the meat upon the p4, I hypothesize that the carpolestids tested would fragment meat better than any other species tested here. Also, dentitions of both *Nycticebus coucang* and *Tarsius spectrum* produced many small fragments when masticating chicken breast meat. Based on my qualitative observations, no species other than those mentioned was able to fragment meat effectively.

8.5.6 Fruit

The fruits tested were problematic because they are very watery and relatively heterogeneous. Furthermore, this group is very heterogeneous as it includes food with diverse structural properties. On average, fruit was well fragmented. The biological role of many fruits is to attract mobile predators that will consume the nutritious, fleshy pulp and carry the inedible seed (embryo) elsewhere. Therefore, the mechanical properties of

fruit likely correspond to the mechanical abilities of the teeth of their dispersal agents. It is not surprising then that most fruits were well fragmented in this experiment.

Though juniper cones may not be homologous to angiosperm fruit, I placed them in this category because their physical properties are similar to those of true fruit. Juniper cones possess an skin that is tough and relatively pliant. Within, fibrous pulp surrounds an extremely hard seed. Juniper cones were usually fragmented well. They were usually split open within a few chewing cycles and fibrous components were progressively reduced to smaller fragments. The seed was often expelled and denuded of fibrous material. Only two dentitions broke the seed itself: *Loris tardigradus* and *Nycticebus coucang*. *Phenacolemur praecox* and *Carpodaptes hazelae* were also reasonably adept at fragmenting juniper cones. Most other dentitions were moderately successful, though some dentitions (e.g., ‘Pointy’) succeeded only in denting them.

Plum chunks were very well fragmented by most dentitions. These items were generally split in half along the long axis of the tooth row. The peel proved very resistant to tearing, though when initiated, cracks propagated readily through it. The pulp itself deformed readily under minimal loads, but it was only separated into discrete pieces by the action of blades on the teeth. The structural properties of the pulp change considerably as the plum ripens; therefore, I used only plums of the same degree of ripeness. These were quite firm.

Most dentitions successfully divided plum pulp. However, discrete pieces of pulp were often held together by peel if the peel remained untorn. Both carpolestids successfully tore both peel and pulp using the blade-like p4. Nevertheless, such a blade can only make one division per chewing cycle; whereas a multi-bladed molar could conceivably make several. According to my qualitative observations, *Tetonius matthewi* is the most successful fragmenter of plum, though there is little interspecific variation noted. Flatter dentitions tend to mash plum chunks such that plenty of juice is expressed but fragmentation is minimal. The expression of juices from a fruit could be considered more adaptive than the fragmentation of the fruit; however, this value is not quantified here. The quantification of juice expression requires more stringent controls on water loss than were exercised in this experiment.

Elderberries and barberries have similar structural properties. They both possess a tough skin that envelops primarily liquid contents and two or three very hard seeds. The skin of the barberry is thicker, tougher and more brittle and its seeds are somewhat harder than those of the elderberry. Barberry skin was usually split preferentially along the long axis of the berry. The liquid content of both berries is significant. Both berries were well-fragmented by most dentitions. Elderberries were fragmented more successfully than barberries. Generally the skin was torn and liquid was expressed. Seeds were expelled but generally not broken, though there were some exceptions. Elderberry seeds were broken by 'Flat', *Phenacolemur praecox* and *Tupaia glis*. Barberry seeds were never broken and usually adhered to the peel via several fibrous strands. The most proficient fragmenters of barberries were 'Flat' and *Otolemur crassicaudatus*. The plagiualacoid p4's of both carpolestid dentitions were successful at slicing into berries, but were unsuccessful at separating them into fragments.

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Chapter 9: Discussion

9.1 Introduction

The purpose of the mastication experiment was to generate data on the differential food fragmentation capabilities of several primates. Assuming extinct primates were optimised with respect to dietary anatomy and assuming a tight relationship between dental morphology and diet, these data can be used to infer dietary preference. Without the benefit of gut contents, ‘fragmentation capability’ or ‘masticatory performance’ is the most powerful tool available for paleodietary inferences. This is particularly true – as for many plesiadapiform species - when no good modern dental analogue exists.

In the following descriptions, I make several inferences about the diets of extinct primates. These inferences are wholly based on the various values of masticatory performance described in Chapter 8. Just because a particular species performed well on a particular food in my experiment does not necessarily mean that the species in question was a habitual consumer of that food. Masticatory performance is but an *approximation* of diet. Note that diet, defined as such, is the diet to which teeth are best suited structurally.

If the results of the mastication experiment are taken at face value (see Chapter 8 and Appendix 2), then it appears that the test species are adapted to eating nuts, seeds and fruit more than anything else. This may be the case. However, these foods may be, *in general*, less resistant to fragmentation. I suspect that the latter is true because species of extant primates that eat almost no nuts, seeds or fruit (e.g., *Loris tardigradus* and *Tarsius spectrum*) masticate them very well nonetheless. The structural properties of the foods I used in the experiment could be tested in order to compare their resistance to fragmentation in general. Further study in this area should include such tests.

Because of uncertainty about the general properties of the test foods, I have based my dietary inferences on primarily the doubly averaged values for all measures of masticatory performance. Each doubly averaged value represents the deviance (and the direction of the deviance whether positive or negative) of the raw value for a given species-food pair from the mean for the food in question and the mean for the species in question (see Chapter 8). When doubly averaged values are used, it is easier to see variation among the poorer performances. Regardless, the ranking of species performances for a given food is not changed by doubly averaging, nor is the ranking of foods for a given species.

9.2 Dietary differences between major taxonomic groups

Many primatologists operate under the assumption that the earliest plesiadapiforms were insectivores (e.g., Cartmill, 1972; Gunnell, 1989). Some even believe that the earliest euprimates were insectivores (e.g., Cartmill, 1972). Compared to the extant insectivores tested, most of the plesiadapiforms and extinct euprimates tested would *not* be inferred as insectivorous based on masticatory performances. As for all other dietary inferences, this is based exclusively on masticatory performance. Of the extinct test species, only the euprimates *Notharctus* sp. and *Arapahovius gazini* appear to be adapted to eating insects. In general, plesiadapiform test species perform more poorly on insects than do euprimates. Therefore, assuming the initial plesiadapiform was an insectivore, a dietary shift *away* from insects had already occurred in the Plesiadapiformes by the late Paleocene.

The Eocene euprimates tested were significantly better at breaking down insects than were the plesiadapiforms tested ($p < 0.001$, see Table 8-1). This supports the claim (Cartmill, 1972) that the emergence of the euprimates was marked by a shift toward greater insectivory. The euprimates are also better at breaking down fruits than are the plesiadapiforms, though the difference is insignificant ($p > 0.10$). Thus, the angiosperm co-evolution hypothesis (see Sussman, 1991) is supported, but weakly so. Proponents of this hypothesis need not despair, however. Two of the eprimate test species, *Tetonius matthewi* and *Smilodectes gracilis*, appear to have been adapted to breaking down fruit, whereas *Notharctus* sp. and *Arapahovius gazini* were adapted to breaking down insects. It is possible that some lineages became frugivorously adapted in the early Eocene, while others became increasingly adapted to insectivory. Both activities would have taken place in primarily the terminal branches of trees (Cartmill, 1972; Sussman, 1991). This compromise resembles the suggestion by Rasmussen (1990) that the first euprimates were adapted to the consumption of *both* insects and fruit. Perhaps the early Eocene was not only marked by a shift in dietary preference of primates, but also by a shift toward greater dietary specialization. Greater variation exists among masticatory performances of euprimates than among those of plesiadapiforms, though this warrants further testing. The Eocene euprimates tested fall into two groups: inferred frugivores (*Smilodectes gracilis* and *Tetonius matthewi*) and inferred insectivore-graminivores¹ (*Notharctus* sp. and *Arapahovius gazini*). Based on masticatory performances, *Cantius eppsi* probably had a diet of mostly nuts and seeds, but also small quantities of insects and fruit. This intermediate condition may be plesiomorphic for Eocene euprimates.

¹ That is, animals that eat primarily insects but supplement the diet with nuts and seeds.

Dietary inferences about major taxonomic groups rely on the assumption that the test species represent them adequately. For the extant primates, this assumption is unjustified because I intentionally chose to test several small, mainly insectivorous species. Accordingly, the extant test species are generally much more insectivorous (and carnivorous) than the extinct ones. Despite the very non-frugivorous character of the extant test species, they fragment fruit much better than do plesiadapiform test species ($p < 0.02$). This suggests that the plesiadapiforms were particularly non-frugivorous (compared to the tested Eocene euprimates and tested extant species). This is a reasonable suggestion; fleshy fruit like the ones tested here do not appear in the fossil record until the early Eocene (Tiffney, 1984). Based on the masticatory performances of test taxa, late Paleocene plesiadapiforms were probably herbivorous generalists. They probably ate small, nut-like diaspores, leaves, flowers and possibly gum. They may also have eaten stems and nectar or other foods not tested here. It is unlikely that they were primarily insectivorous.

The similarity in dietary preferences between any two out of the three major taxonomic groups (extant primates+*Tupaia glis*, plesiadapiforms and euprimates) can be estimated by averaging the absolute values of the differences between the d-values of both groups (Table 8-1, sixth column) for all test foods. This value is 2.78 for plesiadapiforms and euprimates, 3.47 for plesiadapiforms and extant taxa and 3.20 for euprimates and extant taxa. Therefore, plesiadapiforms and euprimates are most similar with respect to masticatory performances, euprimates and extant taxa are somewhat similar and plesiadapiforms and extant taxa are quite dissimilar. This suggests that more ecological continuity exists between the late Paleocene plesiadapiforms and Eocene euprimates than exists between the latter and the extant taxa tested. This may have phylogenetic value if masticatory performance is treated as a metric (i.e., measured) character. In this context, the hypothesis that plesiadapiforms are closely related to and possibly gave rise to euprimates is supported by my data. However, perhaps similar masticatory performance in these two groups arose by convergence and the Eocene euprimates replaced the Paleocene plesiadapiforms. The latter is equally supported by my data. A more rigorous phylogenetic analysis is necessary before definitive conclusions are drawn.

Some have suggested that adapids were adaptively similar to lemuriforms and that omomyids were adaptively similar to tarsiiforms (e.g., Conroy, 1990). The former is questioned based on the significant difference ($p < 0.10$) between masticatory performances of adapids and lemuriforms. The latter is supported by the lack of significant difference between the masticatory performances of omomyids and *Tarsius spectrum*. Nonetheless, performances of adapids and *T. spectrum* were not significantly different from each other either, nor were performances of omomyids and lemuriforms. These minor differences

suggest there may be greater dietary disparity *within* these large taxonomic groups than between them.

Differences in masticatory performance between plesiadapiforms and *Tupaia glis* are significant, but only at the 10% level.

9.3 Plesiadapiforms

9.3.1 *Plesiadapidae*

The plesiadapids tested here performed similarly. They break down fruit, nuts and seeds much better than other test foods. This partly corroborates Gingerich's hypothesis that plesiadapids were herbivores (Gingerich, 1976) as well as Covert's hypothesis that the genus *Plesiadapis* is made up of frugivores (Covert, 1986). It is quite possible (see Chapter 2) that the crenellations on the molars of many plesiadapids are instrumental in pulping fruit, but my experiment is not sensitive to the function of such morphological details.

Of the two species of *Plesiadapis* tested here, *P. churchilli* is somewhat more frugivorous, whereas *P. fodinatus* is somewhat more generalized in its masticatory performance. Neither one is very proficient at fragmenting leaves, insects, meat or gum. Seligsohn's method for inferring diet fails to consider nuts and seeds. The results of my use of his method predicted that both *P. fodinatus* and *P. churchilli* would perform best on fruit (see Seligsohn, 1977 and Chapter 4 of this thesis) and that the latter would prove more frugivorously adapted than the former. This appears to be the case. Using Kay's method (Kay, 1975), I predicted that *P. churchilli* would perform like a dietary generalist, and that *P. fodinatus* would perform *very differently*, probably adapted to eating shoots and stems (not tested here). Using Evans and Sanson's method (Evans and Sanson, 1998), I predicted that neither plesiadapid would be especially adept at breaking down insects, nor would they be especially inept. Furthermore, the results of this method suggest that *P. churchilli* is better adapted than *P. fodinatus* to punching though the ductile² bodies of insects, but that it is less well-adapted to penetrating the brittle cuticle of hard-bodied insects (e.g., crickets). *P. fodinatus* was in fact better at fragmenting insects in general, but it was only better at fragmenting crickets - *P. churchilli* was better at fragmenting the ductile-bodied meal

² The meaning of terms such as *ductile*, *brittle*, *tough*, *fragile*, *strong* and *weak* - as they pertain to food materials - are defined by Strait, 1997. I have attempted to adhere to her definitions as much as possible, though I use them in a purely qualitative manner.

worms. Thus with reference to the Plesiadapidae, the limited predictions made using Evans and Sanson's method are borne out.

9.3.2 *Carpolestidae*

The carpolestids are enigmatic with respect to diet and dental function. Therefore, they make very interesting test subjects. Additionally, the North American species of carpolestids are thought to have become increasingly dentally specialized over time (e.g., Rose, 1975). However, the idea that the carpolestids represent one simple lineage (e.g., Rose, 1975) is no longer tenable. Currently the fossil record of carpolestids in North America is much better known than it was twenty-five years ago and the relationships among carpolestids are known to be complex (Silcox *et al.*, 2001). At least in theory, increasing dietary specialization from an *Elphidotarsius* dental morphology to a *Carpolestes* dental morphology can be tested with a mastication experiment.

The carpolestid species I tested were extremely competent given most test foods. They excelled with all foods except insects. They were able to process all different kinds of vegetation: primarily fruits, nuts, seeds and gum; leaves and flower petals to some degree. This makes sense because there is much specialization *within* the post-canine dentition; with more specialization within the dentition, a greater variety of foods can be processed effectively. Whereas the plagiualacoid p4 is particularly competent at slicing through ductile foods (e.g., soft fruit, meal worms, chicken, gum), the cuspidate molars are competent at cracking very brittle foods (e.g., hard fruit, nuts) (see Chapter 8, section 8.5).

The extremely good performance of *Carpodaptes hazelae* given gum is the sole obvious difference between the performances of the test carpolestids. If *Carpodaptes* is simply a less-specialized version of *Carpolestes*, then this difference is difficult to explain. Perhaps the greater degree of wear in the specimens of *C. hazelae* is responsible. However, for all other foods, these two species performed very similarly. *C. hazelae* fragmented fruit, insects and meat slightly more effectively, whereas *C. dubius* fragments herbaceous foods, nuts and seeds more effectively. In this instance, my classification of food may be deceiving. The competence of *C. dubius* given herbaceous foods and nuts and seeds is mainly due to good performances on ginkgo leaves and maple seeds. These foods are characterized by fracture in a single plane: ginkgo leaves split readily along veins and maple seeds split parallel to the long axis of seed coat fibres (see section 8.5). If *C. dubius* is the culmination of a dental-dietary trend, then perhaps that trend leads to increasing ability to fragment structurally linear foods.

Simpson (1933) suggested that the plagiualacoid dentition of carpolestids was adapted to breaking down coarse vegetation specifically, and plant parts generally. He also suggested that carpolestids were probably best-adapted to frugivory. My data do not refute these hypotheses. Nor do they refute Rose's (1975) hypothesis that carpolestids ate mainly hard fruit and hard seeds or Kay and Cartmill's (1977) hypothesis that they were frugivore-graminivores. Unless my test insects poorly represent the insects available to carpolestids, my data refute the hypothesis that carpolestids were primarily insectivorous (Rose and Fleagle, 1985a).

My data partly refute Biknevicius' (1986) hypothesis that carpolestids ate foods with a soft interior, such as invertebrates, nuts and seeds. Both test carpolestids performed poorly on test invertebrates; however, they performed well on nuts and seeds. Still, I do not see how the interior of a maple seed or a sumach fruit qualifies as 'soft'. The structural property described by Biknevicius is not actually 'softness', but rather ductility. Though the interior of insects and other invertebrates (such as snails) is ductile, the interior of nuts and seeds is *brittle*. The best mastication performances of test carpolestids are on pistachio endosperm and juniper 'berries'. Pistachio is quite brittle and weak: it changes shape very little before fragmenting, but it fragments under low loads. The outer skin and fibrous interior of juniper berries are somewhat ductile, but the skin is very thick and strong (it withstands high stresses). Carpolestids also fragmented leaves and rose petals relatively well. These foods have quite different structural properties from juniper berries and pistachios. They are brittle, tough (resist crack propagation) sheets. Whereas ginkgo leaves and rose petals are weak (i.e., they fail under low stresses), oak leaves are strong. Carpolestids seem able to fragment foods with a wide variety of structural properties - the only foods they do not fragment successfully are those that *do* possess a soft (i.e., ductile) interior. Perhaps the catholic diet of carpolestids can be attributed to 'task-specialization' in the post-canine dentition.

Using Seligsohn's morphometric method, I predicted that *Carpodaptes hazelae* would be a frugivore and that *Carpolestes dubius* would be an insectivore, and that they would perform very *differently*. Neither prediction is corroborated by the experimental results. Neither species is relatively insectivorously adapted. However, *C. hazelae* did fragment fruit more effectively than did *C. dubius*. In contrast to those predictions made using Seligsohn's method, those made using Kay's method suggest that the carpolestid species would perform similarly. Using Kay's method, I predicted also that carpolestids would excel given ductile foods. The first prediction holds true; the second is only partly true. Values of tip and cusp sharpness suggest that test carpolestids, especially *C. hazelae*, are highly adapted to breaking down insects. *Neither* species fragmented insects well: not

absolutely, not relatively. However, *C. hazelae* did break insects more effectively than did *C. dubius*.

It is quite possible that the carpolestids were insectivorous. They were very small, and small mammals generally require insects to furnish them with the protein necessary for their (presumed) high metabolism. Many (e.g., Biknevicius) have suggested that carpolestids *must* have eaten insects because they were too small to effectively obtain protein from leaves. However, *Lepilemur* possesses gut microflora capable of digesting cellulose and is able to live a folivorous lifestyle. *Lepilemur* is a small nocturnal lemur that reingests its faeces to recover digested cellulose; individuals of some *Lepilemur* species weigh as little as 500g (Fleagle, 1988). Although there is no evidence of a similar mechanism in carpolestids, perhaps they too were able to break down cellulose.

9.3.3 *Phenacolemur*

Paleontologists disagree about the diet of *Phenacolemur*. Masticatory performances suggest that *Phenacolemur praecox* ate primarily juicy fruits and nuts. Grain size distribution (see ternary diagrams in Chapter 8) suggests that leaves or petals may have contributed to the diet of this species. The dietary hypotheses of Rose and Fleagle (1985a), Covert (1986), Williams (1980) and Szalay (1972) are all partially substantiated by these results. *Phenacolemur praecox* performed poorly on gum, against the expectations of Kay and Cartmill (1977); however, the gum I tested represents only dried gum, not fresh gum. Contrary to the expectations of Williams (1980), *P. praecox* performed poorly on insects. It is important to note that *P. praecox* is one of the only species that regularly broke juniper seeds and elderberry seeds. These seeds are extremely strong. Perhaps as Szalay (1972) suggested, *P. praecox* broke seeds with its stout premolars. Perhaps this animal also processed soft fruit in its large talonid basins (Rose and Fleagle, 1985a).

All seven indices from Seligsohn (1977) that I applied to *P. praecox* suggest that this species was an insectivore. The results of the fragmentation experiment suggest otherwise. The dietary predictions about *P. praecox* that I made based on my application of Kay's (1975) method are mostly confirmed by masticatory performances. This species possesses long shearing crests for dividing soft fruit and a great deal of horizontal shear for cutting thin leaves and seed shells.

Phenacolemur praecox has very blunt cusp tips. Congruently, this species fragments crickets poorly. However, *P. praecox* has rather sharp cusps. Evans and Sanson (1998) predicted that sharp cusps are good for dividing ductile materials, such as soft fruit and insect viscera; this prediction is partly confirmed by the good performance of *P.*

praecox on soft fruit. *P. praecox* is very unsuccessful at breaking down insects, but this may be because it is unable to penetrate the cuticle.

9.3.4 *Plesiolestes*

The results of all three morphometric analyses suggest that the remaining plesiadapiform, *Plesiolestes problematicus*, was primarily insectivorous. Covert (1986) also suggested insectivory for this species, whereas Szalay and Delson (1979) suggested frugivory and Gunnell (1989) suggested omnivory. In fact, the only foods well-fragmented by this species were pistachios and plums. If *P. problematicus* was insectivorous, it must have been eating insects with very different structural properties from those tested here. The results of the morphometric analyses suggest this might be the case. However, *P. problematicus* performed best on nuts, seeds and fruit. Based on masticatory performances, it is interpreted very tentatively (because all other lines of evidence are against it) to have been a graminivore-frugivore.

9.4 Eocene euprimates

Based on masticatory performances, the Eocene euprimates in this study fall into two broad dietary categories. *Smilodectes gracilis* and *Tetonius matthewi* were probably specialized frugivores (the former more so than the latter). This inference is corroborated by grain size distributions (see Chapter 8, Figure 8-24). *Notharctus sp.*, *Arapahovius gazini* and *Cantius eppsi* were probably graminivore-insectivores (though *C. eppsi* fragmented insects only moderately well). Thus, dietary preference crosses broad taxonomic boundaries in the test Eocene euprimates more so than in the test plesiadapiforms.

9.4.1 *Adapidae*

Notharctus and *Smilodectes* are usually thought to have been folivores (Rose and Fleagle, 1985b; Covert, 1986; Conroy, 1990; Fleagle, 1999). *Smilodectes* is considered the more folivorously adapted of the two (Szalay and Delson, 1979; Covert, 1986; Fleagle, 1999). All of my results suggest that neither species was proficient at breaking down leaves or flowers. However, by most measures, *S. gracilis* was the better of the two (though the difference is very small).

Cantius species are thought to have been frugivores (Covert, 1986; Fleagle, 1999). Though *Cantius eppsi* fragments fruit reasonably effectively (see ternary diagrams), it performed best on nuts and seeds. Compared to other test species, it fragmented very well the highly resistant maple seeds and sumachs. It also processed the juicy barberries and elderberries very effectively.

The six main Seligsohn indices suggest a frugivorous habit for *Cantius eppsi*, *Notharctus sp.* and *Smilodectes gracilis*. This is corroborated by the masticatory performance of *S. gracilis* and perhaps *C. eppsi* (see ternary diagrams), but not of *Notharctus sp.*. Index XXXV suggests that these species were highly insectivorous. This is partly corroborated by the masticatory performance of *Notharctus sp.* but not at all by that of *S. gracilis* or *C. eppsi*.

For all three principal components in my replication of Kay's method, *Cantius eppsi*, *Notharctus sp.* and *S. gracilis* plotted very near the origin. I interpreted these species as dietary generalists. Based on masticatory performance, these species could be construed as dietary generalists, but certainly not when compared to the carbolestids, for example.

All three species have very blunt cusp tips; therefore, relatively poor penetration of the cuticle of crickets is predicted (especially for *Notharctus sp.*). Though the other two species performed poorly on crickets, *Notharctus sp.* performed relatively well. All three species have relatively blunt cusps; therefore, relatively poor fragmentation of larvae and other ductile foods is predicted by Evans and Sanson's (1998) model. This prediction fails in the case of *Notharctus sp.* which is actually the best fragmenter of larvae among all test species. Furthermore, *Smilodectes gracilis* is extremely successful at fragmenting several ductile foods (mainly fruits).

9.4.2 *Omomyidae*

Few dietary inferences have been applied to *Arapahovius gazini* and *Tetonius matthewi*. Covert (1986) suggested that both genera were mainly insectivorous, and that *T. matthewi* may have supplemented its diet with fruit. Szalay and Delson (1979) suggested *T. matthewi* was an omnivore that concentrated on fruit. In fact, masticatory performances, also, suggest that *Tetonius matthewi* was a frugivore. This species also fragmented meat, nuts and seeds moderately well. Compared to other test species, *A. gazini* fragments insects extremely well. It also fragments fruit reasonably well.

Both omomyid species plotted among the insectivores for Seligsohn's index XXXV. *Arapahovius gazini* plotted among the insectivores for Seligsohn's other indices, whereas *Tetonius matthewi* plotted among folivore-frugivores. Thus, Seligsohn indices

accurately predicted masticatory performances of *A. gazini*, but only partly accurately that of *T. matthewi*.

For all factors of my principal components analysis, *Tetonius matthewi* plotted near the origin. This suggests, contrary to the masticatory performances, that it was a dietary generalist. The position of *Arapahovius gazini* on the principal component plots (see Chapter 8, Figures 4-3 to 4-5) suggests it was eating soft-bodied invertebrates and perhaps fruit. This prediction is borne out by the fragmentation data.

Both *Tetonius matthewi* and *Arapahovius gazini* have somewhat sharp cusps and somewhat sharp cusp tips; therefore each species should fragment insects moderately well. It is difficult to assess these dietary predictions against masticatory performance simply because they are so moderate. However, if masticatory performances are accurate reflections of diet, then values of tip and cusp sharpness for *Arapahovius gazini* should be higher. Equally, values of tip sharpness for *Tetonius matthewi* should be lower as it fragmented insects very poorly.

9.5 Extant taxa

The masticatory performances of extant species reflected fairly accurately their true diets. The insectivorous species performed well on insects. *Loris tardigradus*, *Tarsius spectrum* and *Tupaia glis* broke down insects successfully. *Nycticebus coucang* broke down insects reasonably well, but it also performed well on pistachios, plums, juniper cones, elderberries and ginkgo leaves. The folivore-frugivore, *Lemur catta*, performed extremely well on leaves and some nuts, but not very well on fruit. The dietary generalist, *Otolemur crassicaudatus* performed well on rose petals, gum, nuts and seeds; however, the dentition of this species performed poorly on insects. *Loris tardigradus* fragmented meat somewhat better than expected, *Otolemur crassicaudatus* fragmented herbaceous foods and nuts better than expected and *Tupaia glis* fragmented nuts and seeds better than expected.

The masticatory performances of extant taxa suggest that their molars and premolars may be adapted to breaking down the most structurally demanding constituents of their diet (rather than the foods consumed most often or in the greatest proportion). In particular, the test dentition of *Lemur catta* breaks down leaves, but not fruit, very well. Though both kinds of food make up the diet of this species, it is likely that leaves have a greater influence on its premolar and molar morphology because leaves are more resistant to structural deformation. The same could be said for the especially good performance of *Loris tardigradus* on chicken breast muscle and the especially good performances of *Nycticebus*

coucang and *Otolemur crassicaudatus* on hard plant parts. In each case, these foods make up a small, but structurally demanding, proportion of the diet

It is impossible to assess the accuracy of Seligsohn indices for extant species because these species were used to delimit dietary categories for the extinct species.

My replication of Kay's method suggests that *Otolemur crassicaudatus* and *Lemur catta* were dietary generalists. This is partly true for the former; *O. crassicaudatus* eats many kinds of food, especially gum, fruit and insects. *Lemur catta* is known to be a folivore-frugivore, however. *Nycticebus coucang*, *Loris tardigradus*, *Tarsius spectrum* and *Tupaia glis* are all predicted to be insectivores. This is the case.

Both *O. crassicaudatus* and *L. catta* have blunt cusps and blunt cusp tips. Neither is competent at breaking down insects; therefore, Evans and Sanson's idea about the dietary meaning of these features holds true for these two species. The other extant species all have relatively sharp cusps with sharp tips. However, they are certainly not as sharp as expected for these obligate (or nearly so) insectivores.

9.6 Artificial dentitions

Many dietary inferences are based on a cursory, qualitative assessment of molar morphology (e.g., Szalay and Delson, 1979). These inferences usually rely on the assumption that tall, sharp cusps are good for insectivory and that low, blunt cusps are good for frugivory. I attempted to assess this assumption by testing two artificial dentitions on all test foods. One dentition (Pointy) is composed of small points arranged in a generalized primitive primate cusp pattern. The other (Flat) is completely flat. If the above assumption is valid, one would expect the pointy dentition to perform well on insects and the flat dentition to perform well on fruit. In fact, the opposite is the case. The pointy fragmented fruit more effectively than did the flat one; the flat dentition fragmented insects more effectively than did the pointy one. This is particularly interesting because it questions one of primate paleontology's most basic assumptions. The foods best fragmented by both artificial dentitions are nuts, seeds and fruit.

9.7 Relative merits of morphometric methods

9.7.1 Qualitative assessments

The predictive power of each morphometric method used here (see Chapter 4) can be assessed based on three criteria: accuracy, precision and range. An accurate prediction is

one that matches the outcome. A precise prediction is one that narrows in on a very specific outcome. A prediction with a wide range is one that covers all areas under scrutiny: in this study, one that makes predictions about many kinds of food, or that makes predictions about many dental features. An ideal morphometric method is accurate, precise and wide-ranging.

The precision and range of the three morphometric methods can be assessed before experimental testing. Seligsohn's method of inferring diet is wide-ranging: it includes insects, fruit and leaves and measures several features on the upper and lower second molars. However, it is not very precise in its predictions. Kay's method has an equally large predictive range, but it makes very precise predictions; therefore, even before testing, Kay's is a better method of dietary inference. Evans and Sanson's method is the most precise of all, but it has the disadvantage of making predictions over a narrow range of foods for only two very specific dental features. The accuracy of the predictive methods can only be assessed by comparison with either living taxa or simulation experiments.

Assuming the results of the food fragmentation experiment accurately reflect dietary preferences, the predictive accuracy of each morphometric method can be assessed by comparison to those results.

Seligsohn's method predicted diet somewhat accurately for Eocene euprimates and plesiadapids but rather inaccurately for other plesiadapiforms. Seligsohn's original method was not intended for predictions about diet, but rather for discovering dental measurements that correlate to *known* diets. Therefore, I had to use extant species as guidelines to infer diet in extinct species. For this reason, my use of Seligsohn's method did not *predict* diet for extant species. My use of Kay's method predicted diet fairly accurately for carpolestids, *Phenacolemur*, omomyids and extant taxa. Overall, it was a more accurate predictor of diet than was Seligsohn's method. Evans and Sanson's method was the most accurate. It predicted diet very accurately for *Phenacolemur*; fairly accurately for plesiadapids, adapids and extant species; and somewhat accurately for omomyids. This method is the most accurate of the three.

9.7.2 Quantitative assessments

The relationship between morphometric results and experimental results was assessed by a test of correlation, described in Chapter 8. Here I will describe only the strong correlations. No correlations had an r-squared value greater than 0.3. Therefore, none of the measurements used is very strongly tied to masticatory performance (at least for the foods tested). Polynomial correlations (see Chapter 8) are of questionable importance

simply because of the artificial increase in the r-squared value that occurs when the order of the polynomial is increased.

Seligsohn's six main indices correlated strongly with the fragmentation of insects, fruit, gum and meat. The correlation with insects and fruit was predicted by Seligsohn (1977), but he did not examine the role of gum or meat in his study. Therefore, these indices are quite useful for predicting the importance of insects, fruit, gum and meat in the diet of extinct primates. Further testing is required to confirm this conclusion. Seligsohn's index XXXV did not have the predicted relationship with diet. Instead, it correlated strongly with meat only.

Kay's dietary predictions focused on the relative proportions of insects, leaves and fruit in the diet. The only factor in my principal components analysis (based on the method described in Kay, 1975) that strongly correlated with the relative proportions of insects, leaves and fruit in the diet was Factor 1. This principal component (=factor) roughly represents brachydonty. Those species with high scores for Factor 1 have a low, small m₂ with lots of surface for shearing and grinding. Teeth that have low scores for Factor 1 belong to species that fragmented either insects or herbaceous foods much better than they did fruit. This correlation partly justifies the use of Kay's method to infer 'herbinsectivory' in fossil primates. I also examined the correlation between each of the three principal components and fragmentation of each kind of food. There were several moderately strong correlations; these are presented in Chapter 8. For example, species that possess low, small m₂'s with lots of area for shearing and grinding fragmented fruit effectively. Also, those species that possess high, large m₂'s with little area for shearing and grinding fragmented fruit effectively; only those species with intermediate scores for Factor 1 were poor fragmenters of fruit. Factor 2 roughly represents the amount of shear in the m₂ and M₂. Those species that have low scores for Factor 2 fragmented insects effectively. Species that have high scores for Factor 3 possess high m₂'s with lots of area for grinding and M₂'s with relatively little transverse shear. Such teeth belong to species that fragmented herbaceous foods and insects poorly (but see also Figure 8-10). Clearly Kay's method has some power to predict masticatory performances on insects, herbaceous foods (leaves and flower petals) and fruit.

As predicted, tip sharpness and cusp sharpness correlated positively with the fragmentation of insects. However, this correlation was somewhat weak; correlations with the fragmentation of meat were stronger. Also as predicted, tip sharpness correlated positively with the fragmentation of crickets, but negatively with the fragmentation of meal worms (both correlations were weak). Furthermore, cusp sharpness correlated positively with the fragmentation of crickets. However, against predictions, sharp cusps fragmented

meal worms *ineffectively*. Nonetheless, when Evans and Sanson's method was applied to extinct primates, dietary predictions matched masticatory performances very well. Thus, this method has a great deal of predictive power, despite its narrow range of dietary predictions.

9.7.3 Conclusion

Based on both qualitative and quantitative assessments, Evans and Sanson's (1998) method for inferring diet from dental morphology is the most accurate of the three used here. Kay's (1975) method is slightly more accurate than that of Seligsohn (1977). However, accuracy is not everything. Evans and Sanson's method is also the most precise: it makes very specific predictions. Kay's method generates somewhat specific predictions, whereas those generated by Seligsohn's method are rather vague. By contrast, the predictions generated by both Seligsohn's and Kay's method apply to a wide range of foods and dental features. Those generated by Evans and Sanson's method apply to only a few kinds of food and only two dental features.

9.8 Reservations and limitations

Before one accepts the conclusions drawn from a study like this one, one must be prepared to make a few assumptions. I have mentioned my major assumptions where they are most relevant. However, it is instructive to review them here.

The field of functional morphology relies on the assumption of a tight link between form and function for any anatomical structure. Paleodietary studies of mammals generally rely on the assumption that there is a tight relationship between dental form and dental function and that the relationship is driven by dietary preference. Some (e.g., Lauder, 1997) have urged caution in assuming that there is a tight link between the form and function of detailed anatomical structures. However, if this assumption is unjustified, then so is the study of teeth to infer diet.

The principle of uniformitarianism is key to paleontology. That is, the assumption that physical processes at work today pertain equally (or nearly equally) to the past. Thus, if the post-canine teeth of an extinct primate work well to break down a particular kind of food in a mastication simulation today, then they would have broken the same kind of food equally effectively (or nearly so) when the animal was alive. If this assumption is questioned, then so is much of paleontology.

I have assumed that a single modern analogue can be used effectively to simulate mastication in several extinct and extant primate-like species. The analogue I have chosen is

Otolemur crassicaudatus. *O. crassicaudatus* was also chosen partly because its mastication is well-known. The validity of my experimental results rests on the appropriateness of this extant species as a masticatory analogue for all the test species. Clearly this is somewhat flawed; mastication was probably very different in the extinct species tested. However, to isolate the variable of tooth shape (including tooth size), it was necessary to keep mastication and all its variables constant. This is a necessary simplification for a comparative study.

To simulate the muscles of mastication, it was necessary to assume that the physiological cross-sectional area of a muscle is directly proportional to the force it exerts during normal activity. It was also necessary to assume that the activity pattern of each muscle is somewhat parabolic (that is, having a single peak for each chewing cycle with a gradual increase toward peak activity and a gradual decline beyond it) in order to create the cams for my machine. I assumed that steel cables are reasonable approximations for muscles. I also simplified mastication in the machine such that each cycle is the same as the last. Chewing cycles are known to vary based on properties of food (e.g., Hiiemae, 1978), but I kept them constant to assess the effects of various foods on masticatory performance.

When I chose fossil specimens to cast and test, I assumed that if the upper tooth row occluded well with the lower (a purely qualitative judgement), and if the two belonged to the same species, then they were a reasonable approximation for the dentition of a single individual. Furthermore, I assumed that the masticatory performance of that single individual represents the masticatory performance for the entire species. I also assumed that dietary inferences made using only the p3-m3 and P3-M3 are adequate. This is much more dental material than is normally used to infer diet in extinct primates (e.g., the morphometric methods used in Chapter 4).

I assumed that those foods derived from species with family members in the Paleocene and/or Eocene were available to the extinct test primates. In the process of preparing foods for testing, some assumptions were made. I assumed that some food preparation should be simulated, such as the removal of pistachio shells.

When assessing the results of my experiment, I made a further suite of assumptions and approximations. I treated all fragments in a particular sieve as if they were the same size (i.e., the size of the sieve aperture). This assumption is used readily in sedimentology (e.g., Folk and Ward, 1957). I also modelled all fragments as spheres to perform comparisons of surface area to volume. On a theoretical level, I assumed that effective mastication necessarily reduces large fragments to small fragments to increase the surface area for digestion. Finally, I assumed that masticatory performance can be used to approximate dietary preference.

Though all dietary inferences above are stated in an absolute manner (e.g., *Arapahovius gazini* was insectivorous), they are actually *relative* to the other test species (e.g., *Arapahovius gazini* was more insectivorous than most of the other species tested).

Most of the above assumptions are well-founded. Those that are not, are necessary for the experiment to function. The acceptance of these assumptions is crucial to the acceptance of my conclusions. As with all experimental science, the simulated mastication experiment is a simplified version of a biological phenomenon; its results are only as good as its imitation of life.

9.9 Conclusion

The results of the food fragmentation experiment allowed for dietary inferences and assessment of some morphometric methods that are used to infer diet. Little dietary disparity between plesiadapiforms and Eocene euprimates was detected. This suggests that although a dietary shift may have occurred in late Paleocene-early Eocene primates, it was either 1. not very significant, or 2. did not pertain to the taxa tested here. Paleocene plesiadapiforms were adapted to herbivory; they concentrated on nuts and seeds primarily and leaves secondarily. Some adapids and some omomyids were specialized frugivores, as was the late-occurring plesiadapiform *Phenacolemur praecox*. Other adapids and omomyids were insectivore-graminivores. The masticatory performances of extant taxa mimicked their diets; they are mostly insectivores or generalized herbivores. The *Flat* dentition did not perform especially well on fruits, nor did the *Pointy* dentition perform especially well on insects.

The appearance of fleshy fruit in the latest Paleocene-earliest Eocene North American and European fossil record is thought to have sparked the radiation of ‘true primates’ (e.g., Sussman, 1991). The euprimates are also thought to have been adapted to catching and eating insects in the terminal branches of trees (e.g., Cartmill, 1972). In fact, it appears that *some* Eocene euprimates were specialized frugivores and *others* were insectivorous. These ecological categories cross large taxonomic boundaries. The transition from ‘archaic’ primates to ‘primates of modern aspect’ may have been marked by an increase in dietary disparity among primate species. Both the visual predation hypothesis and the angiosperm co-evolution hypothesis are thus partly corroborated by the results of the mastication experiment.

Despite the abundance of insect fauna in the Paleocene and Eocene forests, plesiadapiforms (at least the late Paleocene ones tested here) partook instead of small dry fruiting bodies and perhaps leaves. Perhaps the archaic primates became dispersers of

angiosperm seeds in the Paleocene, when fleshy fruits were rare. This relationship grew over time, and some primates became specialized dispersers (e.g., *Tetonius matthewi* and *Smilodectes gracilis*). Simultaneously, some angiosperms began to develop large, fleshy diaspores to attract dispersers like the euprimates (Tiffney, 1984). Though the latest Paleocene climatic event (Dickens *et al.*, 1997) had an effect on faunal composition, its effect on the ecological niches occupied by primates was probably minor.

The results of the mastication experiment were compared to the results of three morphometric methods that were designed to infer diet from molar morphology. Masticatory performance was assumed to be an accurate reflection of diet, and morphometric methods were assessed against it: their predictive power was examined. Predictions generated using Evans and Sanson's (1998) method were the most accurate, followed by those generated using Kay's (1975) method. Seligsohn's (1977) method was the least accurate. However, Evans and Sanson measured only the sharpness of cusps and the sharpness of cusp tips. These measurements made accurate predictions for only a few kinds of food (insects and possibly meat). Kay's method and Seligsohn's method made predictions for several kinds of food. The predictions generated using Evans and Sanson's method were very precise; those generated using Kay's method were somewhat precise; and those generated using Seligsohn's method were quite vague.

Because each of these methods suffers from important flaws, a combination of methods is advocated here. Alternately, a completely different method, such as one that maps the entire topography of the post-canine teeth, may be used. Regardless, methods that measure dental morphology alone should be checked against experimental methods such as this one. One virtue of experiments in functional morphology is that they examine the *nature* of the form-function relationship.

The results generated by the mastication experiment are significant and predictive. They can be tested by further experimentation (possibly with other extant taxa) or chance finds of exceptionally well-preserved fossils. However, this kind of experiment would benefit from greater quantification of the structural properties of test foods. Machine simulation is a rarely used, but extremely useful method to infer diet. It constitutes an independent test of established morphometric methods and an independent line of evidence for paleodietary studies.

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Appendix 1: Specimen numbers, species names and abbreviations

Abbreviation	Species	Maxilla	Mandible	Side
A.g.	<i>Arapahovius gazini</i>	UCMP 100000	UCMP 115668	R
C.d.	<i>Carpolestes dubius</i>	YPM PU 13275	YPM PU 14077	R
C.e.	<i>Cantius eppsi</i>	BMNH M13773	BMNH M15145	R
C.h.	<i>Carpodaptes hazelae</i>	AMNH 33980	AMNH 33980	L
L.c.	<i>Lemur catta</i>	UCMZ 1975.068	UCMZ 1975.068	R
L.t.	<i>Loris tardigradus</i>	UAAC 972.4.1	UAAC 972.4.2	L
N.c.	<i>Nycticebus coucang</i>	UAMZ 4657	UAMZ 4657	L
Noth.	<i>Notharctus sp.</i>	DMNH 3090	DMNH 13384	L
O.c.	<i>Otolemur crassicaudatus</i>	UAAC 972.9.1	UAAC 972.9.2	R
P.c.	<i>Plesiadapis churchilli</i>	UALVP 42709	UALVP 42708	R
P.f.	<i>Plesiadapis fordinatus</i>	YPM PU 13393	YPM PU 13930	L
Ph.p.	<i>Phenacolemur praecox</i>	USGS 2347	USGS 5986	L
Pl.p.	<i>Plesiolestes problematicus</i>	YPM PU 16588	YPM PU 16591	R
S.g.	<i>Smilodectes gracilis</i>	DMNH 10000	DMNH 10000	R
T.g.	<i>Tupaia glis</i>	UAAC 978.18.1	UAAC 978.18.2	L
T.m.	<i>Tetonius matthewi</i>	UMMP 76675	UW 10212	R
T.s.	<i>Tarsius spectrum</i>	UAMZ 4652	UAMZ 4652	R

Table A1-1 Specimen numbers, species names and abbreviations. Both the pointy and the flat dentition were tested on the right side. The meanings of institution abbreviations are as follows: AMNH, American Museum of Natural History; BMNH, British Museum, Natural History; DMNH, Denver Museum of Natural History; UAAC, University of Alberta Anthropological Collection; UALVP, University of Alberta Laboratory for Vertebrate Paleontology; UAMZ, University of Alberta Museum of Zoology; UCMZ, University of Calgary Museum of Zoology; UCMP, University of California Museum of Paleontology; UMMP, University of Michigan Museum of Paleontology; USGS, United States Geological Survey; UW, University of Wyoming; YPM PU, Yale Peabody Museum Princeton University Collection.

Appendix 2: Raw Ω values and doubly averaged Ω values

	barberry	chicken	cricket	elderberry	ginkgo	gum	juniper
A.g.	0.04446	0.05434	0.65127	0.17491	0.01994	0.00824	0.47817
C.e.	0.37890	0.03776	0.06593	0.50832	0.01517	0.00488	0.06489
C.h.	0.36217	0.14988	0.15040	0.41922	0.07129	0.13289	0.60468
C.d.	0.19627	0.11504	0.14897	0.17351	0.17760	0.01152	0.45111
Flat	0.36221	0.07555	0.20512	0.35887	0.07697	0.00823	0.39159
O.c.	0.77296	0.10160	0.23470	0.50434	0.00570	0.07699	0.17355
L.c.	0.05302	0.11033	0.13022	0.21950	0.21430	0.07347	0.11667
L.t.	0.13107	0.48523	0.98126	0.31526	-0.00002	0.02370	0.33043
Noth.	0.01555	0.00616	0.31096	0.73315	0.02660	0.00900	0.11598
N.c.	0.13777	0.10257	0.39766	0.53988	0.14163	0.02062	0.41720
Ph.p.	0.20942	0.07423	0.13946	0.50963	0.06256	0.00720	0.32588
P.c.	0.38474	0.02335	0.07175	0.48401	0.00475	0.01458	0.07218
P.f.	0.38431	0.12995	0.30167	0.64627	0.09314	0.03351	0.16218
Pl.p.	0.13207	0.01711	0.08482	0.16149	0.07317	-0.00001	0.20935
Pointy	0.02561	-0.00002	0.03277	0.41545	0.00000	0.00156	0.00002
S.g.	0.41000	-0.00002	0.03107	1.19015	-0.00003	0.00020	0.15996
T.s.	0.16626	0.18750	0.29931	0.23852	0.14232	0.00618	0.11087
T.m.	0.27336	0.14002	0.05866	1.31673	0.01995	0.00391	0.21605
T.g.	0.11078	0.03651	0.96709	0.39370	0.07604	0.07063	0.33352
	larva	maple	oak	pistachio	plum	rose	sumach
A.g.	0.09226	0.12384	0.02199	0.81650	0.16624	0.01651	0.11310
C.e.	0.14471	0.29221	0.00000	0.98837	0.26073	0.06342	0.16904
C.h.	0.18579	0.14440	0.08542	1.53221	0.39522	0.20567	0.18080
C.d.	0.05030	0.21772	0.08427	1.44718	0.26634	0.12482	0.10747
Flat	0.14236	0.02854	0.02265	0.84399	0.43863	0.01225	0.14714
O.c.	0.17370	0.16747	0.01616	1.43505	0.08824	0.49026	0.15741
L.c.	0.12006	0.21942	0.18462	1.26115	0.29360	0.08509	0.05923
L.t.	0.35443	0.20516	0.01359	1.31034	0.31172	0.05036	0.12443
Noth.	0.45285	0.18374	-0.00001	1.48393	0.36378	-0.00003	0.06466
N.c.	0.09695	0.11505	-0.00001	1.60863	0.43775	0.08771	0.14653
Ph.p.	0.13897	0.14145	0.05113	1.65052	0.43082	0.04065	0.09434
P.c.	0.14219	0.06065	0.02201	0.57004	0.96550	0.02728	0.02985
P.f.	0.13242	0.08294	0.01035	1.18712	0.77759	0.04929	0.13270
Pl.p.	0.08769	0.05977	0.05307	1.22033	0.36595	0.04081	0.09192
Pointy	-0.00001	0.00344	0.03493	0.61579	0.42435	0.00000	0.01647
S.g.	0.03572	-0.00018	0.00581	0.24562	0.47927	0.03889	0.00865
T.s.	0.06083	0.11238	0.06757	1.33215	0.14398	0.09915	0.07157
T.m.	0.06610	0.17523	0.02747	0.24539	1.48033	0.04690	0.12456
T.g.	0.44285	0.55242	0.09580	1.59687	0.40260	0.02369	0.15782

Table A2-1 Raw Ω values for all species and specific foods. See Appendix 1 for abbreviations of species names. Each value is the mean of five observations.

	barberry	chicken	cricket	elderberry	ginkgo	gum	juniper
A.g.	0.04158	0.06331	0.74868	0.17170	0.02386	0.01845	0.26237
C.e.	0.49297	0.06287	0.07842	0.22246	0.02083	0.01094	0.05226
C.h.	0.25533	0.02523	0.04021	0.16057	0.06078	0.05372	0.17087
C.d.	0.10581	0.02968	0.07054	0.08703	0.15652	0.01132	0.24836
Flat	0.37151	0.05444	0.18463	0.16539	0.07638	0.01638	0.22020
O.c.	0.40989	0.08500	0.19241	0.88149	0.01275	0.04520	0.12664
L.c.	0.01798	0.03755	0.08617	0.08663	0.12745	0.03127	0.02612
L.t.	0.16839	0.23767	0.94555	0.14524	0.00001	0.02373	0.09683
Noth.	0.01639	0.01382	0.25563	0.66996	0.04014	0.01274	0.03963
N.c.	0.08835	0.09122	0.25705	0.29466	0.09945	0.02468	0.21420
Ph.p.	0.12082	0.03854	0.08990	0.20451	0.04336	0.00993	0.24302
P.c.	0.12248	0.03458	0.06822	0.10405	0.01062	0.03269	0.05506
P.f.	0.20775	0.08491	0.11468	0.22002	0.13978	0.01983	0.07413
Pl.p.	0.05919	0.02402	0.05726	0.17578	0.07756	0.00000	0.13496
Pointy	0.05725	0.00001	0.06590	0.54085	0.00003	0.00207	0.00009
S.g.	0.10025	0.00001	0.06861	0.86249	0.00002	0.00028	0.11405
T.s.	0.09213	0.08729	0.11707	0.11156	0.06766	0.01118	0.06607
T.m.	0.13527	0.04577	0.05147	0.13541	0.03300	0.00875	0.20431
T.g.	0.06941	0.03897	0.72650	0.26327	0.04871	0.07418	0.15277
	larva	maple	oak	pistachio	plum	rose	sumach
A.g.	0.08610	0.06682	0.01920	0.46512	0.06267	0.02265	0.03744
C.e.	0.17687	0.17955	0.00000	0.57350	0.17490	0.11851	0.12921
C.h.	0.08810	0.06555	0.04273	0.42015	0.44173	0.17501	0.09709
C.d.	0.02955	0.11377	0.07213	0.58497	0.27864	0.13829	0.10680
Flat	0.15105	0.04107	0.02242	0.21440	0.34098	0.02741	0.06035
O.c.	0.09069	0.08923	0.02802	0.82815	0.08951	1.00577	0.05450
L.c.	0.04286	0.04295	0.06431	0.47214	0.07928	0.01628	0.03119
L.t.	0.45277	0.08314	0.03040	0.19429	0.10742	0.03299	0.03720
Noth.	0.34604	0.12172	0.00000	0.45593	0.18215	0.00003	0.01876
N.c.	0.04644	0.09885	0.00001	0.09457	0.14475	0.04124	0.06008
Ph.p.	0.04604	0.09404	0.05058	0.23733	0.10353	0.03986	0.04516
P.c.	0.10004	0.07501	0.02816	0.19801	0.72342	0.03973	0.03158
P.f.	0.05540	0.05559	0.01490	0.25702	0.50076	0.03945	0.06183
Pl.p.	0.12661	0.09704	0.02704	1.00145	0.38818	0.04166	0.02193
Pointy	0.00001	0.00802	0.05408	0.52198	0.27886	0.00010	0.03344
S.g.	0.03319	0.00013	0.01302	0.25942	0.27095	0.08702	0.01682
T.s.	0.03686	0.12407	0.03410	0.37488	0.06254	0.05622	0.01993
T.m.	0.06847	0.17286	0.03989	0.47890	0.80471	0.05763	0.08524
T.g.	0.23264	0.30669	0.08304	0.31940	0.26719	0.03453	0.04716

Table A2-2 Standard deviations for all values listed in Table A2-1.

	herbaceous	nut/seed	gum	insects	meat	fruit
A.g.	0.01948	0.35115	0.00824	0.37177	0.05434	0.21594
C.e.	0.02620	0.48321	0.00488	0.10532	0.03776	0.30321
C.h.	0.12079	0.61914	0.13289	0.16809	0.14988	0.44532
C.d.	0.12890	0.59079	0.01152	0.09964	0.11504	0.27181
Flat	0.03729	0.33989	0.00823	0.17374	0.07555	0.38782
O.c.	0.17071	0.58664	0.07699	0.20420	0.10160	0.38477
L.c.	0.16134	0.51327	0.07347	0.12514	0.11033	0.17070
L.t.	0.02131	0.54664	0.02370	0.66785	0.48523	0.27212
Noth.	0.00885	0.57744	0.00900	0.38190	0.00616	0.30711
N.c.	0.07644	0.62341	0.02062	0.24731	0.10257	0.38315
Ph.p.	0.05145	0.62877	0.00720	0.13921	0.07423	0.36894
P.c.	0.01801	0.22018	0.01458	0.10697	0.02335	0.47661
P.f.	0.05093	0.46759	0.03351	0.21705	0.12995	0.49259
Pl.p.	0.05568	0.45734	-0.00001	0.08626	0.01711	0.21721
Pointy	0.01165	0.21190	0.00156	0.01638	-0.00002	0.21636
S.g.	0.01489	0.08470	0.00020	0.03340	-0.00002	0.55984
T.s.	0.10301	0.50537	0.00618	0.18007	0.18750	0.16491
T.m.	0.03144	0.18173	0.00391	0.06238	0.14002	0.82162
T.g.	0.06518	0.76904	0.07063	0.70497	0.03651	0.31015

Table A2-3 Raw Ω values for all species and general foods. See Appendix 1 for abbreviations of species names. Each value for herbaceous foods is the mean of 15 observations (five ginkgo leaves, five oak leaves and five rose petals). Each value for nuts and seeds is the mean of 15 observations (five maple seeds, five pistachio chunks and five sumach fruits). Each value for gum is the mean of five observations (all gum arabic). Each value for insects is the mean of ten observations (five crickets and five meal worms). Each value for meat is the mean of five observations (all chicken breast). Each value for fruit is the mean of 20 observations (five barberries, five elderberries, five juniper cones and five chunks of plum).

	herbs	nut/seed	gum	insects	meat	fruit
A.g.	0.02050	0.42369	0.01845	0.58243	0.06331	0.22095
C.e.	0.07015	0.49736	0.01094	0.13550	0.06287	0.31080
C.h.	0.11926	0.70797	0.05372	0.06720	0.02523	0.27518
C.d.	0.12456	0.70696	0.01132	0.07283	0.02968	0.21400
Flat	0.05374	0.39154	0.01638	0.16244	0.05444	0.26566
O.c.	0.58653	0.76465	0.04520	0.14541	0.08500	0.53133
L.c.	0.09576	0.60723	0.03127	0.06439	0.03755	0.11013
L.t.	0.03256	0.57163	0.02373	0.77306	0.23767	0.14781
Noth.	0.02508	0.71166	0.01274	0.29640	0.01382	0.42715
N.c.	0.08344	0.72564	0.02468	0.23546	0.09122	0.23956
Ph.p.	0.04252	0.76083	0.00993	0.06734	0.03854	0.19992
P.c.	0.02844	0.28078	0.03269	0.08885	0.03458	0.47374
P.f.	0.08554	0.54648	0.01983	0.12315	0.08491	0.36419
Pl.p.	0.05113	0.77552	0.00000	0.09265	0.02402	0.22663
Pointy	0.03356	0.40694	0.00207	0.04721	0.00001	0.34979
S.g.	0.05027	0.18220	0.00028	0.05087	0.00001	0.57547
T.s.	0.05957	0.64122	0.01118	0.14998	0.08729	0.09198
T.m.	0.04305	0.28066	0.00875	0.05724	0.04577	0.71213
T.g.	0.06309	0.67201	0.07418	0.57877	0.03897	0.22414

Table A2-4 Standard deviations for all values listed in Table A2-3.

	barberry	chicken	cricket	elderberry	ginkgo	gum	juniper
A.g.	-79.5	-58.4	181.4	-38.1	-79.5	-82.5	116.3
C.e.	67.7	-71.8	-72.7	70.7	-84.6	-89.7	-71.8
C.h.	30.5	-0.2	-50.1	6.3	-33.7	169.0	113.0
C.d.	-20.6	-18.3	-43.9	-48.3	73.0	-76.2	78.9
Flat	57.0	-44.2	-16.9	17.3	-22.8	-82.7	66.6
O.c.	184.4	-31.6	-20.3	31.8	-94.7	56.4	-37.6
L.c.	-77.1	-18.7	-47.5	-28.7	114.5	54.0	-50.6
L.t.	-52.9	222.8	225.3	-20.2	-100.0	-52.0	16.2
Noth.	-93.9	-95.7	13.9	111.1	-74.4	-81.5	-55.2
N.c.	-48.6	-30.4	37.3	44.1	33.5	-58.0	52.4
Ph.p.	-18.5	-48.4	-49.6	44.1	-40.0	-85.2	24.2
P.c.	74.1	-82.3	-69.6	67.4	-95.2	-69.2	-67.9
P.f.	45.5	-11.1	5.7	75.7	-11.7	-31.6	-39.9
Pl.p.	-36.8	-86.6	-61.8	-40.0	-23.4	-100.0	-1.6
Pointy	-83.2	-100.0	-79.5	127.6	-100.0	-96.4	-100.0
S.g.	95.8	-100.0	-86.0	341.3	-100.0	-99.6	-24.9
T.s.	-27.0	39.6	23.0	-20.7	43.5	-87.0	-52.2
T.m.	2.7	-4.6	-79.6	254.2	-81.1	-92.0	-20.6
T.g.	-62.1	-76.4	203.3	-7.4	-30.7	41.7	11.3
	larva	maple	oak	pistachio	plum	rose	sumach
A.g.	-46.8	-28.1	-68.2	141.7	-39.6	-85.4	-17.8
C.e.	-19.1	64.5	-100.0	174.9	-9.9	-45.1	19.9
C.h.	-11.4	-30.6	14.8	200.2	4.1	61.2	13.4
C.d.	-73.8	14.3	17.0	247.9	-18.0	3.4	-27.8
Flat	-21.7	-84.2	-67.9	127.2	47.7	-89.5	3.0
O.c.	-15.8	-18.2	-78.2	192.1	-76.1	288.0	-0.1
L.c.	-34.2	21.1	161.3	237.1	-1.7	-27.2	-58.6
L.t.	68.8	-1.5	-81.7	156.0	-18.1	-60.6	-22.0
Noth.	131.5	-5.4	-100.0	241.7	8.3	-100.0	-57.2
N.c.	-52.5	-43.2	-100.0	236.4	21.1	-30.1	-6.2
Ph.p.	-29.7	-27.9	-29.8	271.4	26.0	-67.0	-38.1
P.c.	-19.1	-65.3	-68.4	64.2	243.3	-76.1	-78.5
P.f.	-34.4	-58.6	-85.9	154.2	119.0	-60.5	-14.4
Pl.p.	-47.8	-64.2	-22.4	283.1	39.6	-63.2	-31.5
Pointy	-100.0	-97.3	-42.8	201.8	136.6	-100.0	-84.8
S.g.	-78.8	-100.1	-91.5	-23.1	82.4	-65.0	-93.6
T.s.	-66.2	-37.1	-3.9	266.0	-50.7	-14.5	-49.5
T.m.	-67.5	-13.1	-62.7	-48.2	312.6	-62.5	-20.0
T.g.	103.0	155.4	27.0	183.4	-1.4	-81.9	-3.9

Table A2-5 Doubly averaged Ω values for all species and specific foods. See Appendix 1 for abbreviations of species names. Each value is the mean of five observations.

	herbaceous	nut/seed	fruit	gum	insects	meat
A.g.	-78.5	41.3	-6.2	-82.2	95.6	-56.1
C.e.	-70.6	103.3	37.2	-89.3	-42.7	-68.8
C.h.	19.9	80.7	44.1	173.2	-30.2	4.6
C.d.	36.1	109.6	5.1	-75.6	-52.3	-12.5
Flat	-58.9	36.6	68.2	-82.2	-8.7	-39.0
O.c.	71.8	79.0	29.7	59.3	-12.4	-27.8
L.c.	72.5	89.1	-31.7	56.7	-38.4	-14.6
L.t.	-79.6	40.6	-21.3	-52.1	154.4	221.7
Noth.	-90.8	96.9	14.5	-81.1	77.5	-95.4
N.c.	-22.3	96.3	32.8	-57.1	8.5	-26.1
Ph.p.	-46.2	116.8	38.9	-84.8	-34.8	-44.3
P.c.	-79.1	0.7	133.2	-67.6	-37.8	-79.8
P.f.	-47.8	51.5	75.3	-30.0	-2.8	-5.1
Pl.p.	-34.9	114.2	8.7	-100.0	-48.9	-85.0
Pointy	-82.9	61.8	72.1	-96.1	-85.5	-100.0
S.g.	-81.5	-54.1	220.9	-99.5	-77.8	-100.0
T.s.	10.3	87.0	-33.7	-86.8	-11.1	45.5
T.m.	-66.9	-36.4	213.9	-91.7	-70.4	5.9
T.g.	-37.2	101.3	-8.9	43.1	171.8	-75.6

Table A2-6 Doubly averaged Ω values for all species and general foods. See Appendix 1 for abbreviations of species names. Each value for herbaceous foods is the mean of 15 observations (five ginkgo leaves, five oak leaves and five rose petals). Each value for nuts and seeds is the mean of 15 observations (five maple seeds, five pistachio chunks and five sumach fruits). Each value for gum is the mean of five observations (all gum arabic). Each value for insects is the mean of ten observations (five crickets and five meal worms). Each value for meat is the mean of five observations (all chicken breast). Each value for fruit is the mean of 20 observations (five barberries, five elderberries, five juniper cones and five chunks of plum).

species	food	mean raw Ω value	standard deviation
O.c.	barberries	0.2895	0.1496
Pointy	barberries	0.0166	0.0270
L.t.	chicken	0.5351	0.2886
S.g.	chicken	0.0094	0.0199
T.g.	crickets	0.4217	0.4269
S.g.	crickets	0.0626	0.1179
T.m.	elderberries	0.6618	0.4166
Pl.p.	elderberries	0.3084	0.1522
C.d.	ginkgo leaves	0.2193	0.0914
S.g.	ginkgo leaves	0.0119	0.0376
C.h.	gum arabic	0.1302	0.0852
Pl.p.	gum arabic	0.0125	0.0255
C.h.	juniper	0.5599	0.1685
Pointy	juniper	0.0108	0.0213
T.g.	maple seeds	1.0242	0.3598
S.g.	maple seeds	0.0767	0.0735
L.t.	meal worms	0.5481	0.1800
Pointy	meal worms	0.0773	0.0718
T.g.	oak leaves	0.0813	0.0626
N.c.	oak leaves	0.0582	0.0383
Ph.p.	pistachios	1.9337	0.4940
S.g.	pistachios	1.1489	0.4054
T.m.	plum	0.7424	0.4839
O.c.	plum	0.0715	0.0916
O.c.	rose petals	0.0619	0.0217
Noth.	rose petals	0.0064	0.0089
C.e.	sumachs	0.1394	0.0836
S.g.	sumachs	0.0553	0.0516

Table A2-7 Data from replicate tests. See Appendix 1 for abbreviations of species names. For each specific kind of food, the ‘adept’ species is listed above the ‘inept’ species. Each raw Ω value listed is the mean of ten observations (n=10).

Plate 1. Dental materials and test foods. A-B, methyl-methacrylate casts of primate dentitions that were used in the mastication machine; C-L, foods before (left-hand column) and after (right-hand column) they were masticated by *Nycticebus coucang* in the mastication machine. A, fragment of a left dentary of *Carpodaptes hazelae*, having p3-m3, cast from AMNH 33980; B, fragment of a right maxilla of *Cantius eppsi*, having P3-M3, cast from BMNH M13773. C-D, rose petals; E-F, pistachio; G-H, gum arabic; I-J, meal worm; K-L, barberries. Scale bar = 1cm.



Plate 2. Masticatory muscles of *Otolemur crassicaudatus*. A, lateral view of the head of a thick-tailed bushbaby, dissected to show the superficial masseter and the superficial temporalis; B, ventral view of the same. C, excised masticatory muscles of *O. crassicaudatus* (ORPC 1 female), all from the right side. Top row, left to right: deep temporalis, superficial temporalis, zygomatic temporalis, medial pterygoideus, lateral pterygoideus. Bottom row, left to right: zygomaticomandibularis, deep masseter, superficial masseter, posterior digastricus, anterior digastricus. Scale bar = 2cm.

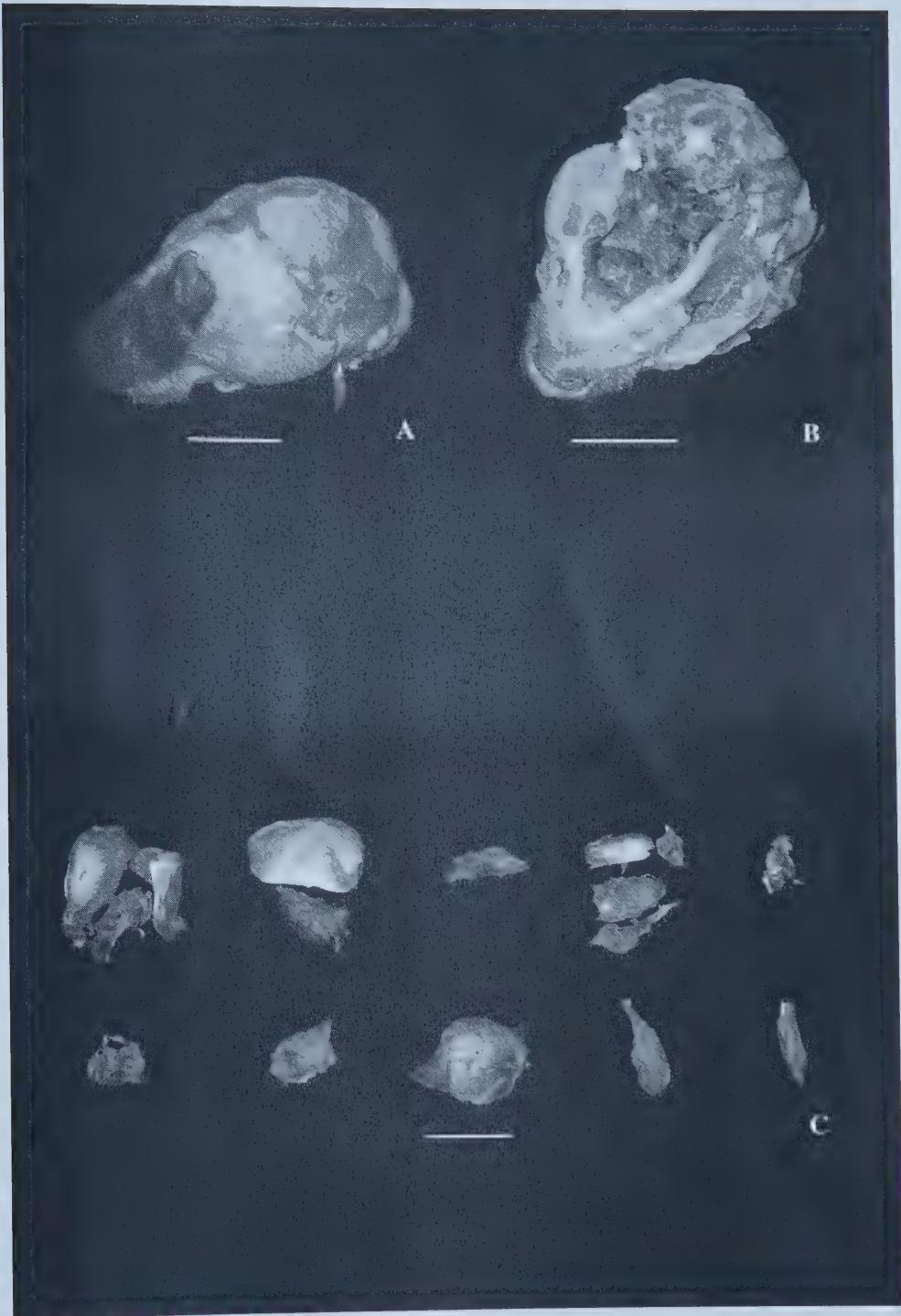
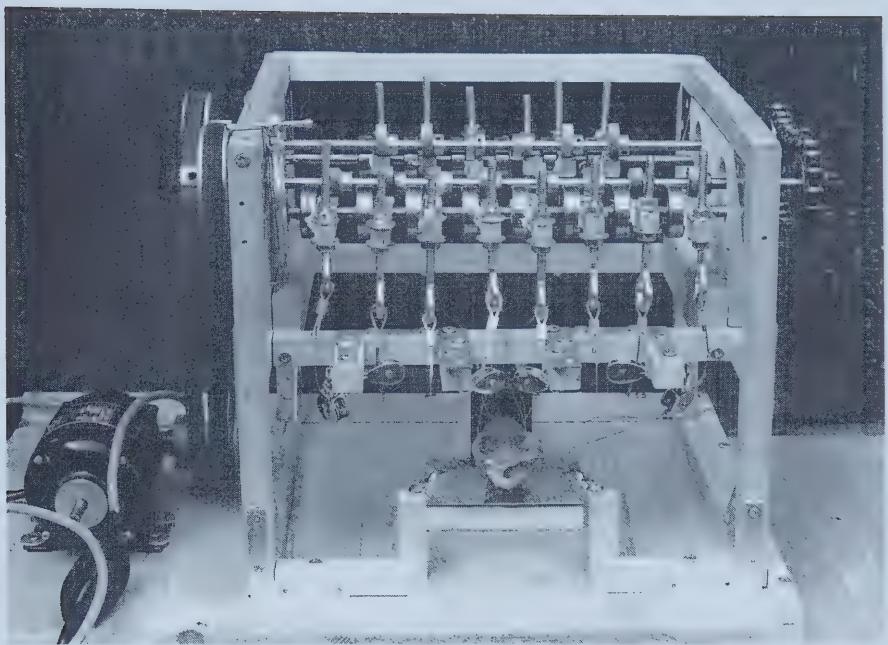
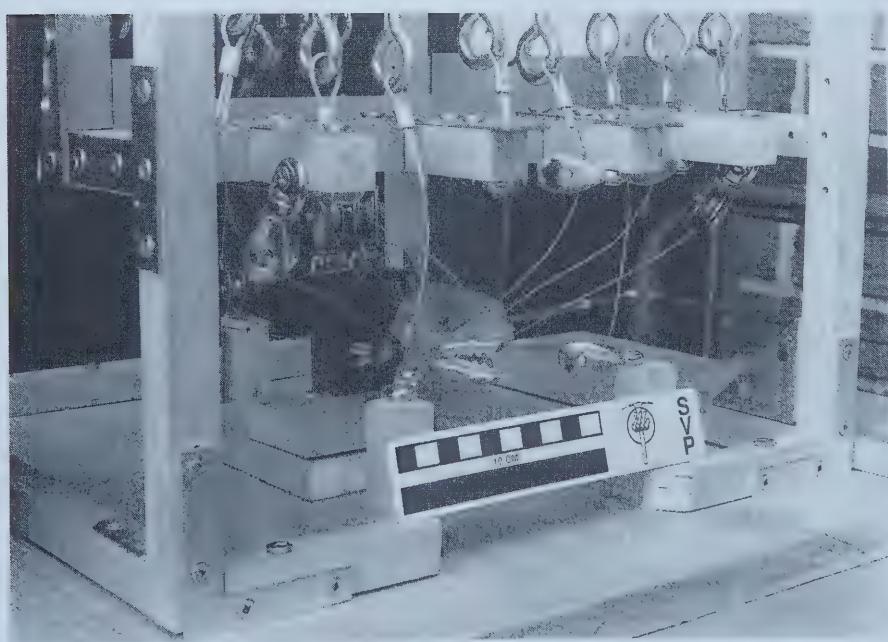


Plate 3. The mastication machine: frontal views. A, the entire machine, long distance view; B, close-up of the skull and attached cables. The methyl-methacrylate dentition of *Lemur catta* (cast from UCMZ 1975.068) is cemented onto the jaw surfaces.

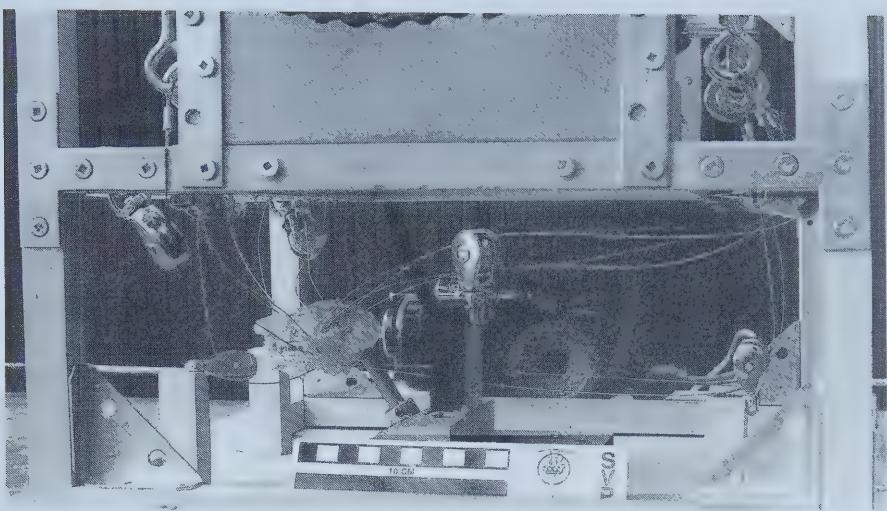


A

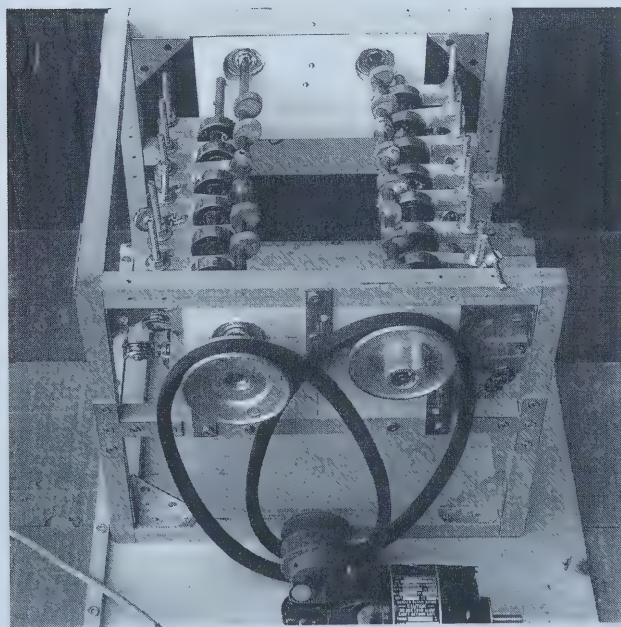


B

Plate 4. The mastication machine: alternate views. A, lateral view, looking at the left side of the machine; B, dorso-lateral view, looking at the right side of the machine.



A



B

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